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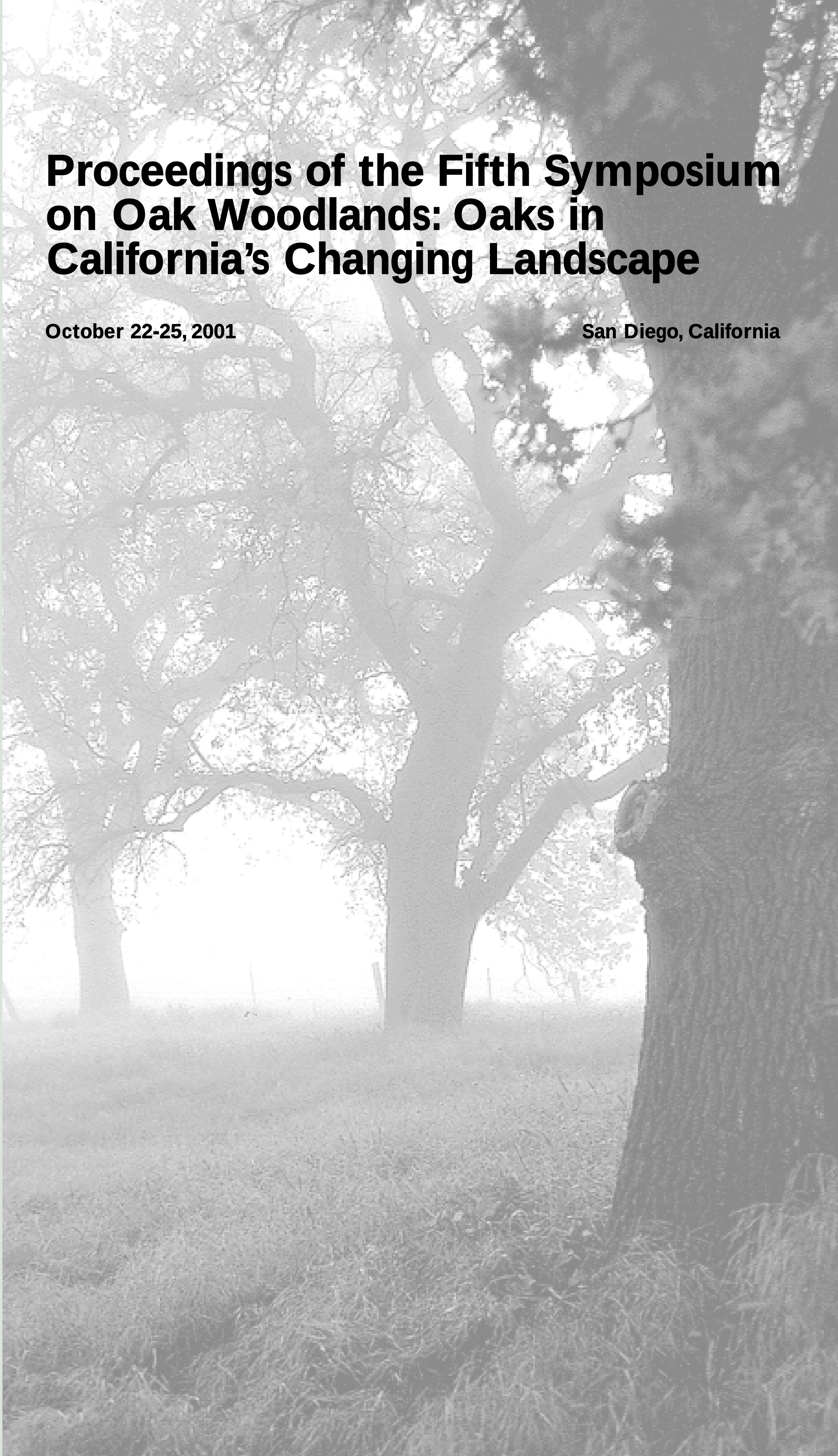

Proceedings of the Fifth Symposium on Oak Woodlands: Oaks in California's Changing Landscape

October 22-25, 2001 **San Diego, California**

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Abstract

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The fifth oak symposium was designed to provide a forum for current research and outstanding case studies on oak woodland conservation and sustainability in California. The previous conferences—held in 1979, 1986, 1990, and 1996—serve as rich sources of information about a wide range of subjects on oak ecology, management, uses, planning and conservation. This conference is aimed at natural resource managers, researchers, policy makers, and public and private interest groups. Seventy-two papers are presented in the proceedings. Topics covered include: grazing relations, soil relations, Garry oak conservation, oak regeneration and restoration, fire relations, wildlife relations, urban forestry, oak woodland policy, genetic factors, monitoring, ecology, and a special session on "Sudden Oak Death."

Retrieval Terms: hardwood rangelands, oak conservation policy, oak sustainability, oak woodland ecology and restoration, sudden oak death

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- University of California Integrated Hardwood Range Management Program
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- California Central Coast Chapter of The Wildlife Society
- California Department of Forestry and Fire Protection, Fire and Resource Assessment Program
- California Native Plant Society
- California Oak Foundation
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- The Nature Conservancy
- Northern California Society of American Foresters
- Society for Range Management, California Section
- Southern California Society of American Foresters
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Contents

The Oak (*Quercus*) Biodiversity of California and Adjacent Regions[1]

Kevin C. Nixon[2]

Abstract

Twenty species of oak (*Quercus*) are known from California. The white oak group is the most diverse, and includes a complex of scrub oak species that are often encountered in chaparral, mixed forest and desert margin habitats. The Protobalanus group (e.g., *Quercus chrysolepis*) is a unique and distinctive clade of western North American species that appears to be most closely related to the white oak group. Within the white oaks and red oaks (black oaks), the majority of California species do not have obvious, close relationships to species outside of the region. In addition, these species either have lobed leaves (e.g., *Q. kelloggii, Q. lobata, Q. garryana*) or have leaves that appear to be derived from ancestors with lobed leaves by reduction (e.g., *Q. dumosa, Q. berberidifolia, Q. john-tuckeri, Q. cornelius-mulleri, Q. agrifolia*). Lobed leaves, such as those found in numerous oaks of the eastern U.S., are characteristic of species from temperate or cold climates, but not any of the more tropical species, thus suggesting a temperate ancestry for the bulk of California oak species in the white oak and red oak groups. In contrast, the Protobalanus group, which is truly evergreen and has entire or merely dentate leaves, probably has a more tropical origin.

Introduction

The genus *Quercus* is one of the most important groups of woody plants in many regions of the Northern Hemisphere. Oaks dominate various temperate, subtropical, and tropical forest types, and are also a major component of several chaparral and scrub vegetations. Although the popular conception of oaks is of a temperate tree that dominates temperate forests of North America and Europe, the center of diversity for the genus in the New World is in the montane forests of Mexico (Nixon 1993a), where oaks species occur as mostly evergreen and semi-evergreen trees, as the sole dominant, or often in association with pine. However, numerous shrub species also occur in association with these forests, sometimes as dominants in chaparral vegetation. Less known are the truly tropical species of *Quercus*, occurring at elevations from near sea level to 1,500 m on both the Atlantic and Pacific slopes, from Mexico to Panama, with one species in Colombia. According to the most recent estimate there are 202 species of *Quercus* in the New World (Fagaceae, in Flora Mesoamericana). Mexico has the greatest number of species (Nixon 1993a; Nixon and Muller 1992, 1993), with ca. 140 *(table 1).* California, with 20 species, is moderately diverse relative to other areas in North America, but is far less diverse than an equivalent sized area of Central or Southern Mexico. Aside from Mexico, other "hotspots" for *Quercus* occur in subtropical-

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[1] An abbreviated version of this paper was presented at the Fifth Symposium on Oak Woodlands: Oaks in California's Changing Landscape, October 22-25, 2001, San Diego, California.

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temperate China and southeast Asia. The southeastern U.S. is another moderate center of *Quercus* diversity, especially the coastal gulf and Atlantic states.

Our present understanding of the generic relationships within family Fagaceae indicates that the genus *Quercus* is monophyletic, and that the genus *Lithocarpus* (Tanoak) is not a part of the *Quercus* clade (Nixon 1984, 1989, 1993b; Manos and others 1993, 1999, 2001). The similar "acorn" fruits of *Lithocarpus* represent independent convergent evolution from more complex multi-fruited dichasial cupules such as found in *Fagus*, *Castanea*, *Chrysolepis* and the trigonobalanoid genera (Nixon 1989; Nixon and Crepet, 1989; Crepet and Nixon 1989a, 1989b; Nixon 1997a, 1997b, 1997c). It is interesting to note that both *Lithocarpus* and *Chrysolepis*, members of subfamily Castaneoideae, are insect-pollinated, while all *Quercus* are wind-pollinated. This difference is reflected in profound differences in flowers and inflorescences between the two groups. Little is known about pollination in California *Lithocarpus*, although small beetles have been observed visiting the flowers (Verne Grant, personal communication), which have an unpleasant odor similar to that of chestnut flowers.

Table 1—*Distribution of* Quercus *species in the New World.*

Area	Number of species	Number of endemics
New World	202	202
Latin America	148	89
Mexico	140	81
Central America	25	8
Costa Rica	14	0
Mexico/Canada/U.S.	194	186
United States	89	46
California	20	7

The California Oaks

The California oaks have been the subject of almost constant taxonomic upheaval for the past century. This is in large part due to improved methods of study but, more importantly, because of more attention to careful fieldwork and consideration of the variation in the context of both morphology and ecological parameters and distribution. Much credit must be given to John Tucker (University of California, Davis, Emeritus) for setting the groundwork for more recent taxonomic studies of California oaks with a series of seminal papers that began to disassemble the broad and variable populations of scrub oaks into component taxa and to firmly establish the hybrid nature of several populations, both widespread (e.g., *Q.* X *alvordiana*) and restricted (e.g., *Q.* X *munzii*). The taxonomy presented here would not have been possible without Tucker's earlier work, as well as the work of the late C. H. Muller, whose interests focused more on Mexican and tropical American oaks. It is satisfying that both of these students of California oaks have been largely in agreement with the newer findings and taxonomy presented here (see Tucker 1993; Muller, personal communication).

The 20 species of *Quercus* found within the political boundaries of California fall into three different Sections (Nixon 1993b, Nixon 1997d): Section Quercus (the white oaks), Section Lobatae (the red or black oaks, often referred to Subg. *Erythrobalanus*), and Section Protobalanus (the intermediate or golden oaks). Within each Section, I have provided only informal groupings that should not be considered to represent monophyletic groups, with the exception of subsection Glaucoideae (see below).

Section Lobatae Red or Black Oaks

1. *Quercus agrifolia* Nee
2. *Quercus kelloggii* Newb.
3. *Quercus parvula* Greene var. *parvula*

   Quercus parvula var. *shrevei* (Muller) Nixon & Muller
4. *Quercus wislizeni* A. DC. var. *wislizeni*

   Quercus wislizeni var. *frutescens* Engelm.

Section Protobalanus Intermediate or Golden Oaks

5. *Quercus chrysolepis* Liebm.
6. *Quercus vaccinifolia* Kellogg
7. *Quercus tomentella* Engelm.
8. *Quercus palmeri* (*Quercus dunnii* is a synonym).

Section Quercus White Oaks

Prinoideae group

9. *Quercus sadleriana* R. Brown, Campst.

Glaucoideae group

10. *Quercus engelmannii* Greene

California lobed-leaf white oaks

11. *Quercus lobata* Nee
12. *Quercus douglasii* H. & A.
13. *Quercus garryana* Dougl. var. *garryana*

    Quercus garryana var. *breweri* Jeps.

    Quercus garryana var. *semota*

California scrub white oaks

14. *Quercus dumosa* Nutt. *sensus stricto*
15. *Quercus berberidifolia* Liebm. (formerly often called *Q. dumosa*)
16. *Quercus john-tuckeri* Nixon & Muller

17. *Quercus pacifica* Nixon & Muller
18. *Quercus cornelius-mulleri* Nixon & Steele
19. *Quercus durata* Jeps. var. *durata*
    Quercus durata var. *gabrielensis* Nixon & Muller

Sonoran scrub oak group

20. *Quercus turbinella* Greene

Additionally, there are two white oak complexes that are sometimes recognized as species but are considered to be derived from hybrid swarms, and possibly are stabilized nothospecies:

Quercus X *alvordiana* (*Quercus john-tuckeri* X *Quercus douglasii*)

Quercus X *acutidens* (*Q. engelmannii* X *Q. cornelius-mulleri*)

Within each section, essentially every possible hybrid combination has been reported for species that occur sympatrically. There are absolutely no verified cases of hybridization between species from different sections within the California oaks. Outside of California, very few intersectional hybrids have been claimed to have been produced experimentally, but these reports have not been verified with modern genetic or molecular methods. Therefore, until proven otherwise, it must be assumed that intersectional hybrids do not occur in the wild.

California oaks inhabit and dominate a large number of habitats, and have become symbolic of the Californian region. The majority of species are evergreen or subevergreen. This is especially true of the species of the Protobalanus group (e.g., *Q. chrysolepis*), which have leathery leaves that may persist as green, functional leaves for several years. This can be easily seen even in herbarium specimens, and the persistence of leaves for more than 2 years is unusual in the California region and is probably restricted to Protobalanus and the white oak *Q. sadleriana*. When evaluating leaf persistence from either a phylogenetic or ecologic perspective, it should be noted that juvenile oaks, as well as stump sprouts that exhibit “juvenile” growth, often have leaves that have a more leathery, spiny form, and much longer persistence than typical adult foliage. In some cases, species which exhibit leaf persistence of only 12-18 months in adult trees may produce leaves that persist for 24-36 months on stump sprouts and saplings (e.g., *Q. virginiana*; Nixon 1984, 1997).

Relationships of California Oaks

Currently, there are no explicit phylogenies, either morphological or molecular, that treat the California oaks in any detail. This problem is compounded by the large number of species within the genus outside of California that must be considered as potential relatives and therefore included in any thorough analysis. A recent broader molecular analysis of *Quercus* using the ITS and matK genes (Manos and others 2001) included some species of California oak, but resulted in almost no relevant resolution, and is highly suspect due to problems with paralogy in the ITS gene (Vazquez 2001; see also Sanderson and Doyle 1992). It is possible to say at this point only that each of the three sections that occur in North America is likely to be monophyletic based on both morphological and molecular data. Molecular and morphological analyses that include California species are ongoing, but for the present, we can only make inferences about relationships based on the occurrence of specific character complexes that might be considered synapomorphies (shared, derived diagnostic features) for particular groups. Such speculations should be taken as a basis for developing sampling strategies for further work on the phylogeny of California oaks and as a general framework for evaluating the ecological parameters within the group.

Another issue that is relevant to the production of a phylogeny for California *Quercus* is the propensity of oaks to form hybrid swarms, with the result that it is unlikely that the evolutionary patterns among interfertile species are fully hierarchic. Such deviations from regularly divergent patterns may result in lack of resolution in cladograms, in large variances in positions of taxa, and/or results that seem improbable based on other data. In any case, the presumed mode of speciation (or lack thereof) in *Quercus* argues for cautious interpretations of any presumed phylogenetic patterns, whether derived from formal analyses, or merely based on the occurrence of a few characters as is the case in most of the discussions presented here. It is possible that for any given species of *Quercus*, past hybridization has produced a pattern of relationship to other species that is not hierarchic, and cannot be fully expressed in any hierarchic branching diagram. The resolution of such questions awaits more intensive study of the genus at the molecular level, and perhaps the development of novel approaches to data analysis.

Section Lobatae (The Red or Black Oaks)

The "Evergreen" Red Oaks of California—The California red (or black) oaks comprise one deciduous, lobed-leaf species, and three evergreen (or subevergreen) species. Because of the mild climate of California, close proximity to Mexico, and the sclerophyllous evergreen habit of *Q. agrifolia*, *Q. wislizeni*, and *Q. parvula*, one might expect that the closest living relatives of these species would be among the evergreen species of Mexico. However, based on morphological data, there appear to be no obvious connections between the California red oaks and the Mexican red oaks. The California red oaks have a series of features that are not known in Mexican oak species. In general, the sclerophyllous evergreen oaks of Mexico are either truly entire, completely lacking teeth, or have simple teeth, with one tooth per secondary vein. There are a few exceptions to this pattern of venation, both in the white oaks and red oak groups (e.g., the *Q. crassifolia* complex), but none of these species show any particular other features that would suggest a relationship to the California red oaks. While the relationships of *Q. wislizeni* and *Q. parvula* remain ambiguous, the relationships of both *Q. agrifolia* and *Q. kelloggii* seem to be with temperate lobed-leaf red oaks. *Quercus agrifolia* has a leaf venation pattern that appears to be derived from a lobed-leaf form, while *Q. parvula* and *Q. wislizeni* do not. This suggests a possible relationship between *Q. agrifolia* and *Q. kelloggii* or another extinct lobed leaf red oak. *Quercus agrifolia* and *Q. kelloggii* often form hybrids where they are in contact, which tends to be at the lower elevational limits of *Q. kelloggii*.

Quercus wislizeni—Quercus wislizeni (often incorrectly spelled *wislizenii*) is a rather straightforward species that inhabits dry slopes of interior valleys, often in association with the white oak *Q. douglasii*. The leaves are entire or toothed *(fig. 1)*. The most problematic aspects of this species are the extensive swarms of putative hybrids with *Q. agrifolia* and *Q. parvula* var. *shrevei* that occur in the Bay Area (discussed below under *Q. parvula*), where interior valley habitats and more coastal habitats interdigitate more freely due to lower elevations in the Coast Ranges than occur to the south. In southern California, from the Transverse ranges south, *Q. wislizeni* does not typically attain tree stature, and usually has numerous trunks. These populations appear to be genetically distinct and separable as *Q. wislizeni* var. *frutescens*. It should be noted, however, that various individuals and small populations of *Q. wislizeni* var. *wislizeni,* particularly in the foothills of the Sierra Nevada, may have a scrubby form, which seems more environmentally induced.

Figure 1 *Quercus wislizeni* , typical leaf from lower side. Palomar, San Diego County.

Quercus parvula—Confusion persists about the species status *Q. parvula*. This species is highly distinctive and separable from *Q. wislizeni* on the basis of several characters including twig and bud pubescence, leaf form, and acorn shape and size (Nixon 1980, Tucker 1993). The shrubby populations (*Q. parvula* var. *parvula*) are restricted to Santa Cruz Island and a few populations in mainland Santa Barbara County (Nixon 1980, Nixon and Muller 1994). The tree form (*Q. parvula* var. *shrevei*) is a straight tall tree of relatively mesic habitats, often found on the margins of coast redwood forests (*Sequoia sempervirens*) extending within the fog belt from the Santa Lucia Mountains to a few localities north of San Francisco. In contrast, *Q. wislizeni* is a species typical of drier interior slopes and foothills. However, several populations of evergreen red oaks from the Bay Area and northward exhibit a morass of conflicting characters, indicating a hybrid swarm between *Q. parvula* var. *shrevei* (the mainland coastal tree form of *Q. parvula*) and both *Q. agrifolia* and *Q. wislizeni* (Nixon 1980). Apparently these problematic populations were the basis of the synonymy of *Q. parvula* under *Q. wislizeni* by the eastern North American oak taxonomist Jensen (1997) in his treatment of the red oak group for Flora North America. It should be noted that *Q. parvula* var. *parvula* in common garden cultivation with *Q. wislizeni* at Davis, California, and in the hot Central Valley, maintain the distinct features, including habit, leaf, twig and acorn characters, typical of *Q. parvula* in coastal habitats (J. Tucker, personal communication). The features that separate *Q. parvula* from *Q. wislizeni* in remote populations are as great or greater than almost any pair of species of North American *Quercus*, and the occurrence of intermediates, even in large swarms, is not unusual, even between species considered to be only distantly related. The evidence overwhelmingly supports the conclusion that the contact and subsequent hybridization between *Q. parvula* and *Q. wislizeni* are secondary events, and that the two species have a separate history and should be recognized as distinct.

Quercus kelloggii—Quercus kelloggii, the California black oak, is a winter-deciduous species with deeply lobed leaves reminiscent of the lobed-leaf red oaks of Eastern North America *(fig. 2)*. It is mostly restricted to higher elevations, except in the north Coast Ranges. No particular eastern species of lobed-leaf oak is particularly close to *Q. kelloggii* in morphological features, and its overall relationships must await further study.

Figure 2 *Quercus kelloggii*, typical leaf from above. Palomar, San Diego County.

Section Protobalanus (The Golden Oaks)

The Protobalanus group of oaks is mainly restricted in range to the southwestern U.S. and adjacent Mexico. Trelease (1924) considered this group to be intermediate in most features between the red oaks and the white oaks. It is perhaps the most distinctive group of North American oaks, and appears to be more closely related to the white oak group than to the red oak group, based on both morphological analyses (Nixon 1993) and molecular analyses (Manos and others 1999, 2001). All species in this group are truly evergreen, with leaves persisting more than 1 year, and often as many as 3 years. Fruition is biennial as in the red oak group, but because the branches bearing fruit often do not grow in the second year, specimens may appear to have annual fruit and thus may be called "pseudoannual." This condition may be a result of resource allocation, and is seen in various Mexican red oaks as well as California *Lithocarpus*.

Quercus tomentella—Quercus tomentella, the "Island Oak" is restricted to the larger Channel Islands, and also is found on Guadalupe Island off the coast of Baja California, Mexico, the type locality for the species. It is a tree species that resembles *Q. chrysolepis* in general form, but has larger, thicker leaves with more prominent regular teeth and a somewhat corrugated leaf blade *(fig. 3)*.

Figure 3 *Quercus tomentella*, specimen from type locality, Guadalupe Island, Mexico (*Cerda 2*, MEXU).

Quercus chrysolepis—Quercus chrysolepis is the most commonly encountered member of the Protobalanus group in California. It tends to grow in moist canyons and on steep north slopes, hence the common name "Canyon Live Oak." The leaves of *Q. chrysolepis* are distinctive, with numerous golden glandular hairs when young, but becoming glaucous with age *(fig. 4)*. Extensive hybridization has been reported between *Q. chrysolepis* and *Quercus vaccinifolia* in the Sierra Nevada, with *Quercus palmeri* in Arizona, and in isolated pockets on the Channel Islands with *Quercus tomentella*.

Figure 4 *Quercus chrysolepis*, lower leaf surface of young leaf, with glandular hairs. Palomar, San Diego County.

Quercus palmeri—Much confusion surrounds the correct name for this species, which in some of the older literature was called *Quercus dunnii*. The latter name was proposed by Kellogg only as a provisional name, and is not valid under the rules of nomenclature. Although *Q. dunnii* was later accepted by the author, in the meantime *Q. palmeri* had been published as a species and therefore it is the oldest valid name for this species. *Q. palmeri* is a rarely encountered species in southern California, and is more common in parts of Central and Western Arizona, and in Baja California, Mexico. This bimodal Arizona-Baja California distribution may indicate a preference for summer rains, and explain the spotty California distribution as mostly due to attrition with an increasing Mediterranean climate. The leaves of *Q. palmeri* are among the spiniest of any oak species, and the species produces thickets that are virtually impenetrable by large mammals such as humans.

Quercus vaccinifolia—*Quercus vaccinifolia*, or the huckleberry oak, is a low shrub of high montane areas, mostly on the west slope of the Sierra Nevada. It bears a strong resemblance to the shrubby Mexican endemic *Quercus cedrosensis,* found from near the California-Mexican border south, to the closed-cone pine forests of coastal Baja California, and also on higher elevations on Cedros Island.

Section Quercus (The White Oaks)

The ”Prinoideae” group—*Quercus sadleriana* is a rather unique shrub species of the Siskiyou region of northern California that is truly evergreen and has toothed leaves with regularly-spaced secondary veins reminiscent of some eastern North

American species such as *Q. montana* (often called *Q. prinus*; see Nixon and Muller 1997).

"Lobed-leaf White Oaks"—*Quercus lobata*, *Q. garryana*, and *Q. douglasii* are deciduous trees with deeply to moderately lobed leaves (although some individuals of *Q. douglasii* may have unlobed or essentially unlobed leaves, either entire or more commonly irregularly toothed). Within this lobate group, *Q. garryana* shows strong similarities to *Q. gambelii*, a Rocky Mountain species that tends to form multiple trunks. The shrub varieties *Q. garryana* var. *breweri* and *Q. garryana* var. *semota* both are very suggestive of the habit (and montane habitat) of *Q. gambelii*. It is likely that the *Q. garryana-gambelii* complex represents a vicariant distribution of a more widespread ancestral species that has been fractionated with drying trends in the climate of the western U.S. since the Tertiary.

"Scrub White Oaks"—The scrub white oaks (*Q. dumosa sensu lato*, *Q. "turbinella*" and *Q. durata*) have been a source of taxonomic controversy and confusion. A simple interpretation of this problem is that leaf form is highly convergent in scrub oaks, and traditional taxonomies relied too heavily on leaf form without attention to other features, in particular acorn morphology and leaf vestiture. This resulted in a very broad concept of *Q. dumosa* throughout the state. More recent studies, beginning with Nixon and Steele (1981), began to detect a pattern of variation in features of the trichomes, acorns, and habitat that suggest at least 5 species should be recognized from the traditional *Q. dumosa* complex: *Q. dumosa sensu stricto*, *Q. berberidifolia*, *Q. john-tuckeri*, *Q. cornelius-mulleri*, and *Q. pacifica* (Nixcn and Steele 1981; Nixon and Muller 1994, 1997). Each of these species has a very distinctive set of characteristics, and a specific geographic range, as discussed below.

All of the California scrub white oak species (with the exception of the eastern *Q. turbinella*) have a leaf form that appears to be derived from a lobed leaf, as evidenced by the typically branched secondary veins, multiple marginal teeth associated with each secondary vein, irregular tooth spacing, and often deeper sinuses separating groups of teeth derived from each secondary *(fig. 5).* In other words, these species often have leaves that appear to be small lobed leaves in which the sinuses have been reduced to minor indentations. In contrast, the numerous scrub oaks of the interior southwestern U.S. and mainland Mexico generally have secondary veins that are not highly branched, more typically one tooth per secondary vein, and regularly spaced teeth without obvious variation in depth of sinuses separating the secondaries. Without any complete and robust phylogenies for American *Quercus*, the interpretation of these patterns remains speculative, but strongly suggest that the California scrub oaks were derived directly from lobed-leaf ancestors in common with such species as *Q. garryana*, *Q. lobata*, and *Q. douglasii* (and this species may present a good model for a transition to a smaller, less lobed leaf).

Quercus dumosa Nutt. *sensu stricto*—The type specimen of *Q. dumosa* was collected by the well-known naturalist Thomas Nuttall during the voyage that was the subject of the book *Two Years Before the Mast* (Dana 1840). The type locality is listed as "hills near Santa Barbara" and indeed material similar to the type specimen occurs locally in the foothills that are now part of Santa Barbara, such as on the upper grounds of the Santa Barbara Botanic Garden. This material differs markedly from the common forms of more interior localities that have traditionally been called *Q. dumosa*. Several characters separate the type material of *Q. dumosa* from the widespread species now called *Q. berberidifolia* (Nixon and Muller 1997). These characters are significant in the context of oak systematics, and populations bearing these characters are found only in very restricted habitats in low hills near the coast, often on very loose sandstones or granitics, in association with species often referred to as "soft chaparral," as opposed to the "hard chaparral" habitat of *Q. berberidifolia* in higher and more interior localities. One of the most distinctive features of the species is an erect, usually twisted, multi-rayed trichome on the lower leaf surface *(fig. 6),* unlike any other scrub oak. *Q. dumosa sensu stricto* is perhaps one of our rarest and most threatened species, known only in these coastal habitats from Santa Barbara County south to northern Baja California. It is unknown from the Channel Islands. Many of the habitats where *Q. dumosa* would be expected have been destroyed by development, and represent some of the most expensive and desirable real estate in southern California. Because of the former wider application of the name *Q. dumosa*, there probably has been some confusion and resistance regarding the rare status of this species. Anyone doubting the distinctness of the species is encouraged to visit Torrey Pines State Park, in San Diego County, one of the last remaining populations that is relatively intact and accessible.

Figure 5 *Quercus dumosa* , lower leaf surface, and sublobate form. Specimen from 32 km north of Ensenada, Baja California Norte, Mexico (*Wiggins & Gillespie 3999*, MEXU).

Quercus durata—Quercus durata is the only American species of *Quercus* that has a restricted distribution on serpentine. Prior to the naming *of Q. durata* var. *gabrielensis* (Nixon and Muller 1994), the species could be considered a true serpentine endemic, and this can still be said of the population referred to var. *durata*, from Santa Barbara County northward. *Q. durata* var. *gabrielensis,* differing in having larger leaves, a more open growth form, larger abaxial leaf trichomes, and more glabrate upper leaf surface, occurs on open gneiss-derived barren soils in the

San Gabriel Mountains of Los Angeles County. Further ecological work is needed to determine if var. *gabrielensis* is edaphically restricted, and the chemical nature of the soils on which it occurs. The nature of the leaf and twig pubescence, acorn shape, size, and cup morphology, as well as the sublobate leaves of *Q. durata,* suggest a possible relationship with *Q. garryana* and *Q. gambelii*, two deciduous tree species with lobed leaves and probably temperate affinities.

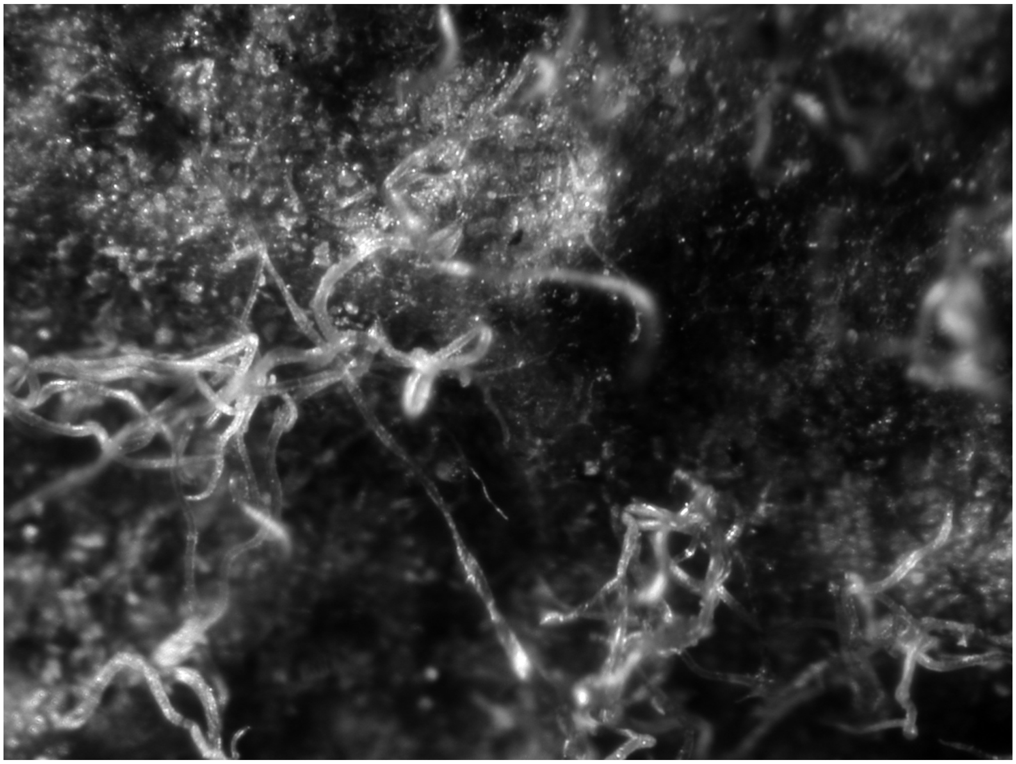

Figure 6 *Quercus dumosa*, sparse, erect, curly trichomes of lower leaf surface, as viewed through dissecting microscope. Field of view is ca. 2 mm across. (*Wiggins & Gillespie 3999*, MEXU).

Quercus berberidifolia—*Quercus berberidifolia* might be considered the "default" scrub oak of the Coast Ranges of Central California. While probably closely related to *Q. john-tuckeri* (formerly called *Q. turbinella* var. *californica*), it occupies more mesic habitats than that species and than *Q. cornelius-mulleri*. It occurs on a variety of soils, while *Q. durata* is restricted to serpentine soils from Santa Barbara County to the north (*Q. durata* var. *gabrielensis* occurs on non-serpentine, but barren gneiss soils, in the San Gabriel Mountains of Los Angeles County). Diagnostic features of *Q. berberidifolia* include the typical usually 7-8 rayed flat stellate trichomes of the lower leaf surface (in contrast to twisted, erect trichomes of *Q. dumosa sensu stricto* and the much larger erect, straight trichomes with fewer rays, found in both varieties of *Q. durata*), a relatively flat waxy leaf with a squarrose or rounded-attenuate base (in contrast to the tapered or acute base and spatulate leaf of *Q. pacifica*), and a usually barrel-shaped, rounded or blunt acorn (in contrast to the sharply acute acorns of both *Q. dumosa sensu stricto* and *Q. pacifica*). Hybrids and/or suspected hybrids occur wherever the scrub oaks come into contact, and given the wide distribution of *Q. berberidifolia*, it is not surprising that putative hybrids occur with *Q. dumosa sensu stricto* (e.g., Santa Barbara County, at mid-elevation and ridges above populations *of Q. dumosa*) and with both *Q. john-tuckeri* and *Q. durata*.

Quercus cornelius-mulleri—Quercus cornelius-mulleri was the first of the four segregate species of *Q. dumosa sensu lato* to be recognized. The nature of the vestiture of the lower leaf surface, with dense whitish stellate trichomes that are microscopically fused into plates, is one of the most prominent features of this species *(fig. 7).* However, it is easily recognized by the dense neat habit, large-tapered cylindric fruit, and bicolored leaves, whitish on the lower surface *(fig. 8).* It is restricted to dry washes and slopes, mostly on granitics and sands, in the interior desert margins and Juniper and Piñon woodlands of San Bernardino, Riverside and San Diego Counties, south into northern Baja California. Among the best places to observe this species are in Joshua Tree National Monument and along most of the east-west roads in San Diego County on the western margins of the Colorado Desert in Juniper and Piñon woodlands.

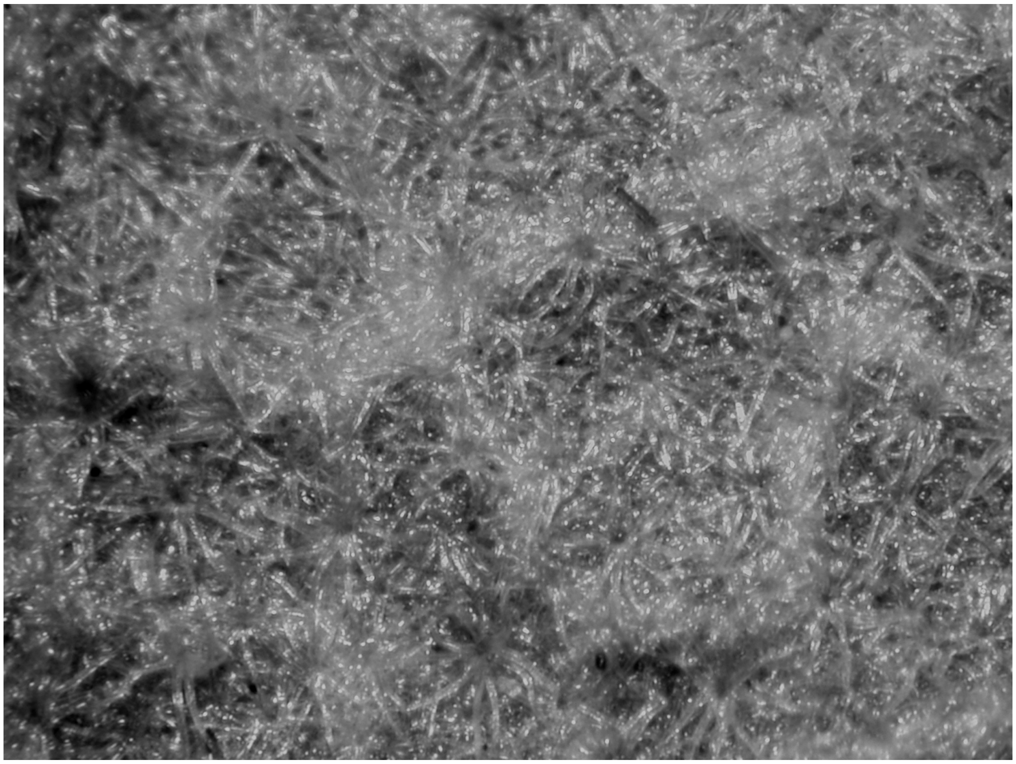

Figure 7 *Quercus cornelius-mulleri*, dense overlapping covering of flat fused-stellate trichomes of the lower leaf surface, as viewed through dissecting microscope. Field of view is ca. 2 mm across. (*Bourell, Patterson & Timbrook 2960*, MEXU).

Figure 8 *Quercus cornelius-mulleri*, typical leaf, with dense whitish trichomes on lower surface. Photographed near Banner, San Diego County.

Like other California scrub oaks, *Q. cornelius-mulleri* probably is related to a group of lobed-leaf species of white oak. A likely candidate, based on vestiture of the leaves, fruit and cup form, and papery bark characteristics, is the species group that includes the species *Q. sinuata*, *Q. pungens* and *Q. vaseyana,* with a distribution from the southeastern U.S. to Arizona and northern Mexico. However, *Q. cornelius-mulleri* also shares certain features with *Q. lobata*, in particular the large tapered acorns*,* and a relationship with that species cannot be excluded.

Quercus pacifica—*Quercus pacifica* is restricted in distribution to the three channel islands Santa Cruz, Santa Catalina, and Santa Rosa (Nixon and Muller 1994, 1997). It closely resembles *Q. berberidifolia*, but differs in having consistently spatulate leaves with a narrowed leaf base, and acute-tapered fruit, with thinner cups. Leaf vestiture otherwise is similar to *berberidifolia*, but that species has typically square or rounded-attenuate leaf bases and blunter, heavier fruit. It is likely that *Q. pacifica* is phylogenetically close to *Q. berberidifolia* or possibly represents a nothospecies derived from intergradation between *Q. berberidifolia* and *Q. douglasii*. This would be consistent with the widespread occurrence on the channel islands of a lobed-leaf small tree referred to *Q*. X *macdonaldii*, and interpreted to be a stabilized hybrid between *Q. lobata* and *Q. pacifica*, suggesting that widespread hybridization has occurred on the islands between the scrub oaks and either *Q. lobata* or *Q. douglasii*, neither of which occur in abundance, but are found in isolated pockets.

Quercus turbinella and Q. john-tuckeri—The name *Q. turbinella* was previously applied to populations to the east of California (Arizona to Texas, into northern Mexico), as well as to populations in California now referred to *Q. john-tuckeri* (mostly interior Central California) and *Q. cornelius-mulleri* (interior desert margins of southern California). *Quercus turbinella* from Arizona and eastwards has a distinctive fruit, relatively small and borne on a peduncle up to four cm in length. Peduncle length throughout the genus *Quercus* is one of the most useful and consistent characters, and species with elongate peduncles are in the minority (e.g., *Q. robur*, *Q. bicolor*, *Q. virginiana*). While long peduncles are typical of all *Q. turbinella* outside of California, the material previously referred to *Q. turbinella* var. *californica* from Central California has subsessile acorns, as in all other California scrub oaks including *Q. cornelius-mulleri*. Additionally, *Q. turbinella* var. *californica* lacks the distinctive cordate leaf base of typical *Q. turbinella* from the east, and has a host of other more subtle differences, such as thicker, more warty cups, larger, blunter fruit, and trichomes with fewer rays. The Californian material is thus better referred to another species, *Q. john-tuckeri*, which in fact seems to be more similar to the other California scrub oaks such as *Q. berberidifolia* than to typical *Q. turbinella* from Arizona. Examination of leaf form in *Q. turbinella* from Arizona and Mexico also reveals that it has more regular, evenly spaced veins that are not suggestive of a lobate form, in contrast to *Q. john-tuckeri,* which has the typical sublobate form found in other California scrub oaks. Interestingly, there are a few populations of typical *Q. turbinella* in the eastern desert ranges of southern California near the Arizona border, and in Baja California on the eastern slope of the Sierra Juarez and Sierra San Pedro Martir. All of these areas receive significant summer rainfall, and it is likely that the range *of Q. turbinella sensu stricto* is determined by the occurrence of summer rain – further negating the idea that it is conspecific with *Q. john-tuckeri*. The relationships of *Q. trubinella* clearly are with a complex of species to the east, including *Q. ajoensis*, *Q. hinckleyi*, and possibly *Q. toumeyi*, none of which occur in California.

Quercus engelmannii—*Quercus engelmannii* is a relatively common component of open oak woodlands in mostly interior foothill localities from Los Angeles County (along the foothills of the San Gabriel Mountains) south to similar habitats in Baja California Norte. Although leaf color is variable in this species, most individuals have a bluish cast to the leaf on both surfaces, and some individuals are strikingly blue in color *(fig. 9)*. Because of the superficial similarities between *Q. engelmannii* and the more northern *Q. douglasii* in leaf color and habitat preference, many California botanists have assumed that the two species are closely related. This is not the case. Numerous morphological features indicate a close relationship between *Q. engelmanni* and *Q. oblongifolia*, a very similar species of oak woodland habitats in Arizona, New Mexico, and northern Mexico. *Q. engelmannii* and *Q. oblongifolia* share a more or less identical leaf vestiture, coloration, shape and size of leaves, and an important complex of embryological features. Both species exhibit marked fusion of the cotyledons in the seed (Nixon 1984, 1993a, 1997d), a feature not found in any other species of California oak, and definitely lacking in *Q. douglasii*. In turn, based on several features including the apparent synapomorphy of fused cotyledons, *Q. engelmannii* and *Q. oblongifolia* belong to well-marked clade of about 35 species of *Quercus* from the southwestern U.S. and Mexico, placed in subsection Glaucoideae. A significant number of these species (e.g., *Q. arizonica*, *Q. perpallida*, *Q. depressipes*, *Q. glaucoides*) exhibit glaucous, often bluish leaves in common with *Q. engelmannii*. *Quercus douglasii* is not a member of the Glaucoideae and evidence suggests a closer relationship between it and the California scrub oaks and lobed-leaf white oaks, such as *Q. garryana*. Thus, the bluish color and habitat preference shared by *Q. engelmannii* and *Q. douglasii* should be considered to be convergent.

Figure 9 *Quercus engelmannii*, branch with acorn. Photographed near Palomar, San Diego County.

The complex of species to which *Q. engelmannii* belongs (subsection Glaucoideae) generally occurs in relatively arid areas that receive most rainfall in the summer months. These localities, from the southwestern U.S. to southern Mexico, are some of the driest places that oaks are found in North America. Additionally, the embryological features separating this group are associated with a germination syndrome in which the embryo axis is placed more deeply into the soil, and may be an adaptation to drought, fire, or both (Nixon 1984). Further study of the ecology of the unusual germination syndrome of this group, including *Q. engelmannii*, is needed.

Summary

The 20 recognized species of California oaks include representatives of 3 major lineages, generally treated as sections within *Quercus*. One of these sections (the white oaks) is widespread in the Northern Hemisphere of both the Old and New Worlds and is the most diverse group within California oaks. The higher diversity of the white oak group in California is consistent with its higher diversity in general in arid areas, in contrast to the red oaks. The red oak group includes only four species, one of which (*Q. parvula*) appears to be a relict of wetter coastal habitats both on Santa Cruz Island and the mainland. The third section, Protobalanus, is endemic to the southwestern U.S. and northwestern Mexico, and is perhaps the most distinctive group of North American oaks. Within the white oaks, the scrub oak group is most problematic taxonomically, and the component species (with the exception of *Q. turbinella sensu stricto*) exhibit leaf morphologies that suggest derivation from one or more lobed-leaf deciduous ancestors. This favors the interpretation that the scrub white oaks were derived from temperate oak ancestors, and are not closely related to scrub oak species of chaparral and woodland habitats to the east and south in summer rain areas of the southwestern U.S. and Mexico. These origins may have ecological significance and should be taken into consideration whenever California oak species are compared with each other, or with species from other areas. One of the best established phylogenetic relationships among California oaks is that of *Q. engelmannii*, often considered to be related to *Q. douglasii*, but which actually belongs to a distinctive group of mostly Mexican species (subsection Glaucoideae), many of which share a bluish leaf color. Members of the Glaucoideae have a unique seed morphology and germination syndrome that may be related to fire or drought adaptation, and which may be important in understanding the ecological parameters controlling the distribution of *Q. engelmannii* in California.

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Perspectives on Cultural Values of California Oaks[1]

Paul F. Starrs[2]

Abstract

The status and prospects of oaks—those native to California and the many elsewhere—are insufficiently known, despite historical volumes of work done in the past and more ongoing today. That globally there is a blistering diversity of oaks in different environments, and put to distinct uses, is beyond dispute. Less agreed upon, though, is their complex history and the variation in the nature of the oak woodland. Because oak landscapes are so varied, and yet so ubiquitous, perhaps their one single shared feature worldwide is a multiplicity of uses. If individual oaks are cherished, and sometimes known by name, the larger woodlands that they comprise are ecosystems of formidable complexity. That is known; what is not is how best to value oak woodlands—and California's in particular. Different attempts have been made; what is crucial to the continued well-being of California's oak woodlands is coming up with some scheme that makes valuation credible, shareable, inclusive, and understandable.

Introduction

What's an oak worth, and why? We start, perhaps, with the single solitary oak, standing in isolation as a first forlorn beacon of possibility, but auguring a once far-larger past presence. But how, then, to value an entire woodland of oaks, a feature that has altogether another aspect? Or even more, what of an entire cultural and economic way of life, a community that goes with the woodland? The issue of putting a value to oaks, considering how a dollar figure or even a tribute to their ecological or spiritual worth might be set, is hardly an insignificant question, especially for a gathering such as this Symposium on Oak Woodlands.

The stories in California alone of setting a value for oaks are legend, of course, and I haven't the least doubt that you could identify appropriate examples. But to start the race, consider these few cases: A handsome oak on a Marin County property adds a cool $50,000 to a starter-castle's sales value, even in the halcyon pre-dot-com days; the town council of Dublin pays out $70,000 to build a steel support for one oak downtown (Davis 2002). In fact, Rick Standiford and Tom Scott have work already going that documents the value of individual or localized oaks (2002).

Or contemplate the rerouting of that long-planned road through a gated community in the Diablo Valley, realigned at astronomical cost, to avoid impinging on the roots of a particularly choice oak specimen. A conservation easement to a well-wooded East Bay ranch, through sales of development rights, is taken on to protect no fewer than eight different species considered to be of "essential" value,

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and funds from the transaction permit another ranching generation to stay on the land. And never does the lingo of the realtor or developer trill better or more loudly than when the bragging words "oak" or "ranch" can be added to an estate or subdivision's name.

These examples demonstrate that the values of oaks are often as much spiritual or aesthetic as pecuniary *(fig. 1)*. Those who seek to understand oaks as a landscape element need to recognize these diverse cultural values if we want to ensure that oaks continue to persist. Many things to many people; that's the oak. But why, then, is the woodland slowly waning? It's a supply that can't meet demand. And creating an oak woodland is truly a long-term effort. After the effects of "rangeland clearing" and other state-initiated hardwood range modifications of the post-World War II era, oaks have become increasingly rare. Those remaining are prized.

Figure 1—No happenstance is afoot in the naming of the Church of the Oaks in Cotati; the juxtaposition of faith with long-lived trees is a human practice of considerable duration. (Photograph by P. F. Starrs, 2000)

Contemplating the value of oaks, especially in cultural merit, is a dicey undertaking, made especially so by an abysmal abiding ignorance about what nature is innately worth. Oaks and the values they embody are remarkably complex: On their own they have existence value; they have a separate scale and stature and ledger for their products; and woodlands collectively have worth as an entire ecosystem. Good luck figuring out the value of the whole of an "ecosystem"—in that there is waiting someone's Nobel Prize in economics. Yet as parts or entire, a woodland of oaks is highly sought after, and few elements of a natural system have such diverse values individually, but so murky a pricing scheme as a whole. An oak is worth something determinable as a live tree or as firewood or as habitat or as an acorn source, but even some of those numbers are contradictory: a live tree can't also be felled as firewood. There is further value of the oak as wildlife habitat, as carbon sink, as biodiversity. While the single oak has a calculable value, the oak woodland is so capacious, so complex, that it's difficult to appraise its price in an enduring, agreed-upon, and universal way. The constituencies and valuations are diverse.

In this, oak woodlands are not that unlike other valued elements of a natural system. For instance, from the 1930s to the 1950s, the loss of soil from American farmlands was a topic of vast scholarly concern; how to document the cost of soil loss, and how to invest in the arresting of soil depletion? With the 1960s and *Silent Spring,* pesticide use became an obsession; in the '90s, the bogeyman became biodiversity's diminution. We might do well to consider conservation and *Quercus* as a millennial concern—and thankfully, many of you associated with oak conservation already have. But at what cost and who is to bear those costs *(fig. 2)*?

Figure 2—The considerable size and reach of valley oaks has done little to reduce their susceptibility to development and clearing; although livestock find alluring their shade and canopy, it has been left up to planners and ordinances to attempt enduring protection. (Photograph by P. F. Starrs, 1988)

Costs and Returns

The fact is that actually going through the processes of setting a value for oaks isn't something we are particularly good at. Ongoing is significant work by Rick Standiford, Pablo Campos, Lynn Huntsinger, and others toward the "total economic value" of oak woodland sites (Campos and others 2002). But so far—and that may change for the better—such studies constitute but an added tool on the economist's belt, rather than a key indicator for the student of cultural studies. Sure, we "like" oaks, we "value" oaks, we "cherish" oaks, oaks are officially part of some towns' "heritage," and are central in many a subdivision's name. We even name towns after oaks—Oakville, Oakdale, Fair Oaks, Live Oak, Paso Robles, Encino, or, in a charming if singular case, “Bellota,” after the Spanish word for acorn. Yet setting an actual value is something far different now than it was seventy-five years ago *(fig. 3)*.

Figure 3—The small community of Bellota, in the Sacramento Valley, has little notion of the significance of its namesake; “Bellota” is the Spanish word for acorn. Nonetheless, around this exurban hamlet oaks abound. The name itself reflects a curiosity about oaks of long duration. (Photograph by P. F. Starrs, 1998)

Certainly our skills as appraisers are bankrupt now as compared to those of our ancestors. They knew what an oak was for, and what it was worth: they knew understory and overstory, fungi and tannin, they understood game animals and acorn mast and forage and branches pruned for conversion to oak charcoal or firewood. Why, we ought to ask ourselves, have we forgotten? What does that say about where our society has gone, and the pathologies of our current deviation from the norm?

Our separation is from the world: that separation as professors, teachers, government employees, researchers, agency personnel, students or ranchers, has brought us to a point where the quite marvelous diversity, productivity, and richness in uses of an oak woodland fails to be foremost in our minds. Buying into a doctrine of parts, we have come to a point where we see not the forest, not even the trees, but only elements of a particular problem: a disease, or a site, or a species, or a fire, or a genome or clade; the grove is part of reductionist science, and indifferent to policy. All but lost is the sheer joy and pleasure in how woodlands look, smell, feel, sound, and taste. Our loss, indeed *(fig. 4)*.

Figure 4—The foothills of the Diablo Range in the East Bay reflect twin pressures of preservation and development as readily as any other California landscape. Not only are orchard crops long gone, the oaks are at risk as the burgeoning development in Alamo, Blackhawk, and other high-ticket suburban communities accelerates with the economic imperative of local growth. (Photograph by P. F. Starrs, 1987)

In 1776, José de Cañizares, a Spanish sailor and accomplished cartographer, produced a map that included detailed (if less than precise) renditions of oaks as a recognizable element of the Bay Area landscape *(fig. 5)*. For these Spanish navigators Alta California was a visually familiar landscape, and for that all the more attractive a stopping-off point. And less than a hundred years later, in 1869, Joachim Richardt delivered a painting that, no less than the Cañizares map, was accurately placed. It showed the oak-draped junction of Madison and 8th Street, in the eponymously-named town of Oakland, California. The point is simple: our perception of the oak woodland, which once involved observing a feature that was visually dominant, has changed from something collective and respectful into an isolated recognition of individual heritage-grade trees. True, many of the great groves are gone, but also because our sense of the whole is supplanted by a view of the single oak as property and commodity.

Think about this description, for instance: “For about twenty miles it could only be compared to a park which had originally been closely planted with the true old English oak; the under wood that had probably attended its early growth had the appearance of having been cleared away and left the stately lords of the forest in complete possession of the soil which was covered in luxuriant foliage” (Vancouver, cited in Pavlik and others 1992). That description, dating from 1796, was of the Santa

Clara Valley, and in the words of British Naval Captain George Vancouver, it was a marvel. We know the area now as Silicon Valley, and changes from one form of use to another were little short of epic. The Dutch geographer Jan Broek, in his 1932 study of the area (Broek 1932), noted the entire Santa Clara Valley was cleared of valley oaks and *Quercus agrifolia* so fruit trees might replace them; in turn those plantings lasted until the 1950s or 1960s, but were then vanquished in favor of pavement, suburbs, and dot-coms.

Figure 5—The Cañizares map, dating from 1776, remains a classic in California; its depiction of the San Francisco Bay Area is recognizable enough, including a small fort at Yerba Buena and a redwood in what is now Palo Alto, but most distinctive are the oaks, evocatively drawn all across the map surface (detail of original, courtesy of The Bancroft Library, Berkeley, California).

About this disappearance of one landscape, the woodland, in favor of another—the urban—there is relatively little written despite the presence, now, of 7 million people, not a few of them quite skilled with words. Yet let me also be quick to point out the vast areas within the San Francisco Bay Area that remain “open space.” Much of that is rangeland, or oak woodlands, that encircle the people resident there. Instead, the changeover rated barely a technical mention in the Census of Agriculture, as “rangeland,” an impossibly badly-defined feature, became “tree crops,” and then disappeared census by census as what John Fraser Hart calls the “perimetropolitan bow wave” wrought its effect (Hart 1991).

The Values Others See in Oaks

What is the intrinsic value of oaks? We haven't really gotten much farther toward resolution, except to point out what hasn't generally been incorporated into the mix. But the aesthetic and nostalgic worth of woodlands isn't anything to minimize. That may sound entirely romantic, but it needn't be. Let me quote, for instance, J. Russell Smith, a professor of geography at the University of Pennsylvania at the turn of the century, who published the very first article, in 1916, in the *Geographical Review,* a journal which, as it happens, I now edit (Smith 1916). In an essay titled "The Oak Tree and Man's Environment," later republished in modified form in an equally classic volume titled *Tree Crops: A Permanent Agriculture,* Smith avers (1987): "If I wanted to be comfortably and permanently rich, I could ask for few more secure bases for it in the line of agricultural lands than the undisturbed possession of a few hundred acres of Portuguese land with a good stand of cork-oak trees (*Quercus suber*) and evergreen-oak trees (*Quercus ilex*). If the stand of trees was good, it would make little difference if the land happened to be rough, untillable hillsides. It would still yield its crops of cork and pork (the pork made of acorns). The virtues of the Portuguese cork forests are quadruple, and the forests are almost perpetual if given a little intelligent care" (Smith 1916, 1987).

He tells of an oak in the Algarve, a grape-growing district of Portugal, also, that yielded 1,200 liters (34 bushels) of acorns; for that matter, yields of a ton of acorns from an oak in the Central Valley of California is not unheard of (Smith 1987). More on point, oak woodland crops in Spain, Portugal, Morocco, France, Greece, and Italy of mast, of wood, of forage, of mushrooms, of corks, of game animals, are anything but unknown. This variegated, quite aged (1800 years, at least), and well-tended Mediterranean landscape is all human—and valued by all (Grove and Rackham 2001). In fact, the European Union's most pronounced effort relating to the Common Agricultural Policy, or CAP, is a move toward what they describe as "low intensity agriculture," in no small measure because of its effectiveness in keeping people on the land, and for its reduction of agricultural waste and overproduction.

Oaks—especially cork oaks—were brought from Portugal and Spain to the United States early on. In fact, Thomas Jefferson made the first known attempt. The Crown Cork and Seal Company and Armstrong Cork later undertook a much more successful effort beginning in the 1880s, and UC Extension Forester Woody Metcalf published on California's cork possibilities in the 1920s and 1930s (Metcalf 1929, 1941). The problem in California turned out not to be climate or fertility, but simply in locating skilled harvesters to strip the cork. Ranchers in California's oak woodlands find many other things to harvest; at least one family ranch the Bay Area makes a respectable income leasing different companies space for cell-phone towers on a hillside facing a busy Interstate highway route in the East Bay *(fig. 6)*. Hunting clubs lease woodlands for habitat; conservation easements can pay off death duties and bring in regular income; carbon sequestration will become a viable income source.

The status and prospects of oaks—here and elsewhere—are insufficiently known, despite huge volumes of work done in the past and ongoing today. That globally there is a blistering diversity of oaks, in different environments, and put to different uses, is beyond dispute. Less agreed upon, though, is their complex history and the variation in the nature of the oak woodland. The literature still develops, and it is voluminous. Because oak landscapes are so varied, and yet so ubiquitous, perhaps their single main shared feature worldwide is a multiplicity of uses. If individual oaks are cherished, and sometimes known by name, the larger woodlands that they comprise are ecosystems of formidable complexity. Nor are crops even in the California oak woodlands in any necessary way limited. Our current distaste, in the American West, for "exotic" trees is newfound; none of California's 350-plus agricultural crops is, after all, "native."

Figure 6—The two slender vertical poles that lie just below the crest, cellular phone transponders, are worth no small amount to the well-positioned landowner and count as another paying use of woodlands. (Photograph by P. F. Starrs, 2001)

A day will come—it is already a fact in the European Union—when landowners will be paid, as a public good, to regenerate oaks on their lands. And why aren't there payments to graze off fire-susceptible areas in the West *(fig. 7)*? In fact, there is the notorious "Goats-R-Us" in the San Francisco Bay Area, which graze the wooded slopes of Sutro Peak (and significant parts of the East Bay Regional Park District), at a fee of up to $700 per acre—remitted to the "Goat Man." Rarely has being a shepherd—or goat rancher—paid so munificently.

My view here, then, is of an expedition into the gray territory of meaning, where the clouded skies of something we call "values" are best clarified by the judicious application of economic, social, political, policy, and larger analysis. No one knows exactly what "values" are—yet the term, with all its indecisiveness, plagues virtually any form of study of humans and their interactions with the world of resources or nature. It has been so since the 1960s, if not before.

Figure 7—With drought and fire ever a part of the California landscape, the results can be spectacular, as at Mt. Diablo in 1977. An ongoing battle over whether to graze parts of Mt. Diablo or to cease grazing has circled, in part, over the fear of park neighbors that a catastrophic fire on ungrazed parklands could leave them with a tinderbox at hand that could not be controlled. (Photograph by J. J. Parsons 1977)

Conclusions

We continue to devote enormous resources to the oaks of California. Witness this conference, the jobs many of us carry out, and the growing efforts devoted to oaks and their sustenance by government, university, NGOs (Non-Governmental Organizations), and landowners. Why do we do this? Why "oaks" and "woodlands," rather than riparian forests, natural levees, madroño or mountain misery? Nothing approaching this degree of attention is directed toward native grasses (though we have some), or to vernal pools, or to relict wildlife populations.

I don't find that question an idle one, nor, probably, should any of us. What are we looking for in our oak woodland work? At some point, monies spread around become part of an elaborate redistribution of wealth, to consultants, to education outreach specialists, to scientists and principal investigators, into the coffers of private science firms or into the purview of university Vice Presidents for Research.

But there is more we can do in our attentions to California's oak woodlands and the values that attach to them. I worry that we concentrate on details at the expense of larger results—arguing about the shape of the germ, not the virulence of the disease. Building blocks are fine, but they are NOT a structure, a building, or even a good plan. Beyond "values" need come action and satisfactory results.

All that is known; what is not is how best to value oak woodlands—and California's in particular. Different attempts have been made; what is crucial to the continued well-being of California's oak woodlands is coming up with some scheme that makes valuation credible, shareable, inclusive, and understandable. We welcome those incoming details. It is time for us to take this knowledge and from that not just ask, but also answer the question: What will California's oak woodlands become?

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Emerging Tools and Institutions to Conserve Oak Woodlands: Integrating Public Trust and Private Benefits, or Can We Ever Get Paid for Doing the Right Thing?[1]

Laurie A. Wayburn[2]

Introduction

This conference on “Oaks in California's Changing Landscape” is a most timely and important conference at a critical time in California. Having been born and raised in California, I have never known a time when this landscape was not changing. And, usually not for the better if you care about our natural environment, as I do. But, today it is changing at an ever-increasing rate and scale, and the forces of restoration and conservation of that natural landscape seem even more outpaced by those of development and degradation.

The facts speak for themselves. Perhaps 45 million acres of California was in forest at the time of settlement, and, of those, some 40 percent or just under 18 million acres were broadleaf, oak and hardwood woodlands (Küchler 1977). By World War II, California had lost one-third of its forests—mostly oak woodlands and hardwood riparian forests—to agriculture and urban development (Wieslander and Jensen 1946).

Today, we have half that number of oak woodland acres, roughly 9.5 million. Perhaps 45 percent of that is so heavily disturbed, built upon, and fragmented with roads, that is cannot function well ecologically, though it may have oaks on it.[3] In fact, California continues to lose forestlands, and at an increasing rate. Every year, California is losing over 60,000 acres of forestland. These are all private forests, with holdings broken up and converted to non-forest. In the five years 1992-1997 we doubled the rate at which we were losing forests compared to the period 1982-1992 (Best and Wayburn 2001, NRI 2001). As documented in the book *America's Private Forests,* which I co-authored with Connie Best (Best and Wayburn 2001), nationwide we are losing roughly one million acres of private forest a year. There is no doubt that, if these trends continue, we will continue to have a rapidly vanishing landscape and a daunting challenge for those who love that landscape and seek to conserve it.

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[3] Unpublished data on file at The Pacific Forest Trust, Santa Rosa, California.

How to Promote Oak Woodland Conservation

How do we change these trends? An essential step is to leverage the love that people have of this landscape with new tools and institutions to conserve oak woodlands and all the values they provide. Effectively, we must integrate the public trust values of these critical habitats with private interest benefits, so that we make conservation and sustainable management competitive with degradation and conversion.

This is what my organization—The Pacific Forest Trust or PFT—seeks to do and, in fact, does, in order to increase conservation of private forestlands. We have directly conserved over 30,000 acres of productive, managed forest, both oak woodlands and conifer forests, and provided conservation planning services on many thousands more acres. Of course, all forests are productive, whether it is productive of habitat or firewood, watershed or residential development, open recreational space or vineyards. But, rather like women, and men, too, who manage households rather than banks, while all are productive, only some get paid for what they produce. And, rather like those household managers who provide great societal and private internal family benefit, those forests producing watersheds, open space, and habitat have great societal and personal benefit, but are not paid for this benefit. In fact, generally the only things which oak woodlands produce that are paid for are those which degrade or destroy them: agricultural conversion and residential development.

So, the things for which we as a society value oak woodlands for are generally not those for which we have an economic value. In the market place, conservation is not currently the driving force for the management of oak woodlands—conversion is. Ecosystem services economies, which theoretically provide trillions of dollars in value, are indirect. They broadly benefit society, but do not directly benefit any individual.

The challenge for us is, therefore, to somehow transform these socially and ecologically essential, but non-economically producing, services of oak woodlands (and, in fact, all forests) into ones which are also economically productive for landowners. This is the nub of the problem: what we as a society want landowners to manage oak woodlands for is not what we as a market pay them for, rather the complete opposite. We want the landowners to do the right thing for oak woodlands, but we pay them to degrade and destroy them.

So, perhaps the real title for my short speech is "can we ever get paid for doing the right thing?"

How can we pay landowners for the intrinsic values and services of oak woodlands—the symbolic values, the scenic, recreational and open space values, the habitat, carbon storing and watershed values of oak forests? Further, can we do so in ways that are compatible with other economic uses such as sustainable ranching or recreation? Collectively, I will term such intrinsic values and ecosystems services as conservation values. Can we create markets for these conservation values such that we can compete with converted oak values such as new residential developments, agricultural row crops, and specialty crops such as vineyards?

There are four reasons to think we can:

1. The substantially increased public concern that we see that led to a greatly increased conservation financing with Propositions 12 and 13 of 2000, and, we hope will give us another in 2002.
2. The increasing development of both public policy and private institutions to work with landowners to restore and conserve working landscapes, ones which work for both private return and public benefit.
3. The increasing awareness of the potential values of forest ecosystems services as watersheds, habitats and carbon storehouses; and
4. The greatly increasing awareness of the risks that global environmental change pose, specifically global warming and intensified water shortages and declines in water quality.

Put together, these four forces are building markets to help pay landowners for the functions that oak woodlands and other forests provide simply through virtue of being oak woodlands: providing watersheds, habitat, climate stabilization and carbon storehouses, and places of recreation.

I am going to discuss these points, including the growing conservation market that public dollars support; government programs that partner with private institutions; and the emerging market values of ecosystems services that will support direct conservation.

Let us look at some examples.

Bond Acts Supporting Conservation

Taken together, the two California bond acts of 2000, Propositions 12 and 13, provided $4.1 billion, with hundreds of millions of dollars in them for land conservation. Much of this money has gone into acquisition of easements for watershed and habitat values held by agencies and land trusts. This coming year, 2002, another Bond Act, AB 1602—the California Clean Water, Clean Air, Safe Neighborhood Parks, and Coastal Protection Act of 2002—is being proposed for $2.6 billion. This new financing is driven by the public's greatly increased desire for open space, clean water, recreation and habitat. These conservation values do not necessarily require a fee-title purchase to be protected; easements are a highly effective tool for this purpose.

As discussed above, many millions of these dollars from Propositions 12 and 13 have gone into land acquisition and the acquisition of interests in land held by agencies and land trusts. You are all familiar with various resource management agencies, but may not be with land trusts, especially those for managed lands, such as the PFT. Land trusts are non-governmental partners in sustainability with private landowners. They are charitable non-profits whose work is private and confidential. They are selected by a landowner to be a guardian of that landowner's vision of forest stewardship.

Conservation Easements

The tool that land trusts commonly use for the acquisition of an interest in land is a conservation easement. I call conservation easements tools for sustainability because they guarantee the future of forestland as forestland. Conservation easements have been in use since the early 1930s, but greatly expanded during the 1990s. Millions of acres are currently being managed under conservation easements. They are an effective alternative to public acquisition in two ways. The public provides compensation to the landowner for a commitment to keep the land in a natural, functioning state; and the forest stays in productive use.

Legally, what is a conservation easement? It is a permanent deed restriction created by a landowner that defines and limits the kind of development and uses for a property. In the cases that I am speaking about, properties are dedicated to forestland purposes—that is, to remain forever as forest or woodland. The easement is voluntarily granted to a non-profit conservation organization, land trust, or government agency selected by the landowner to monitor and enforce the terms.

Why would a landowner create a conservation easement? There are many different landowners and as many different reasons. There is often a strong love of the land and the desire to create a legacy for future generations. They may also want to exercise their rights not to develop, subdivide or over-use their land. Others desire keeping the land in forest while sustaining compatible forest uses. Some want to ensure that future, potentially less well-motivated owners are unable to liquidate the forestland. Some wish to realize financial gains from their stewardship, as the conservation easement can be bought or donated. Further, a gift of conservation easement is the only partial interest gift in real property which is tax deductible. Thus, the government, through this policy enacted in the late 1970s, has promoted nonprofit, private partnerships in conservation.

Now, many of you may think you already know all there is to know about easements, but, unfortunately, a lot of what appears to be known is not, in fact, true.

- *Myth: Restrictions limit future options.* Fact: Only options for houses and asphalt are limited. Options for forests increase.
- *Myth: Sustainable resource management is prohibited.* Fact: Sustainable use is guaranteed.
- *Myth: Environmental activists or state agencies will take over my land.* Fact: No public access is required. Access is by permission and is limited to the monitoring of the conservation easement.

How do conservation easements create financial gain for conservation and sustainable use? In fact, conservation easements are the only partial interest gift in real property that is tax deductible and can reduce the estate valuation, so it is very significant. When valuing a conservation easement, a qualified appraisal of the fair market value of the property is required for a tax deductible gift or below-market sale. Conservation easements provide a means to gain from exercising the right not to develop. The value of the conservation easement is based upon its "before" and "after" valuations, i.e., full market value before the conservation easement restrictions, and a reduced value after the deed restrictions. As conversion and break-up value is so high, eliminating these values has a high reward. Typically we have found that conservation easements reduce values by 30 percent to 70 percent. We will look at an example shortly.

There are costs to creating a conservation easement, including legal and accounting advice; forestry advice; possible forest and other resource inventories; the services of the land trust for the development of the conservation easement and baseline; appraisal; and the stewardship endowment. The stewardship endowment can be a tax deductible gift, or it may be supported by other funding. This stewardship endowment ensures that the Grantee (and Trust) has the means to monitor and enforce the easement through time. A stewardship endowment typically costs less than five percent of the value of the easement, and often as little as 0.01 percent, so it is an excellent investment. Our costs to a landowner, in total, for services and the tax-deductible gift of a stewardship endowment are often $45,000.

Conservation Easement Case Study

So, these are the facts of conservation easements. How are they practiced in real life? A sample easement vignette is the Twining and Oracle Ranches in Mendocino County. These ranches cover 1,524 acres of oak woodland and mixed conifer forest in Talmage, which is in the viewshed of Ukiah. Ukiah is the most rapidly growing city in Mendocino County. It was ranked as one of the ten most livable midsize cities in the United States five year ago, and it has been trying to get rid of that designation ever since by building into the lands that made it attractive in the first place! The primary income source on these ranches is sustainable cattle ranching. The lands are surrounded by vineyards and subdivisions. The Twining and Oracle ranches were donated by Olive Twining with the agreement of her three daughters. Most of the costs of this conservation easement were covered through a grant of financial assistance from the Forest Legacy Program, which is administered by California Department of Forestry and Fire Protection.

The conservation goals on the Twining and Oracle Ranches are to: maintain and enhance the oak woodland and mixed conifer ecosystems; maintain and enhance the native grasslands; maintain and enhance the fish and wildlife habitat and water resources (including a vernal pool and Howell Creek and other tributaries of the Russian River); protect the scenic viewshed for the Highway 101 corridor—the heavily traveled main north/south coastal state highway; and permit sustainable resource uses. These conservation goals are, in fact, constraints on the sources of future economic return. Achieving them without an easement would have meant less available economic return in the short term. Without compensation for that conservation, the Twining family was faced with the unacceptable choice of selling off parts of the ranch. PFT created a conservation easement which allowed them to do what they wanted, yet still compensated them for protecting the Ranch.

The Twining conservation easement is structured to recognize two zones of activity: the Oak Woodland Zone (1,324 acres) and the Development Zone (200 acres). These zones each have different restrictions and permitted uses. The Twinings also reserved the right to keep the property as two ranches, allowing for family control in two pieces, yet treating the land as a whole from a management perspective. They also reserved the right to sell off two small parcels, comprising less than 25 acres located close to the road, if they have to. Within the Development Zone a lot of activity can happen. There can be up to four personal residences; various buildings related to livestock management; the growing of food and crops; cottage industries, transient hospitality, scientific research, and education related to the property's natural resources. Within the Oak Woodland Zone, only grazing and nonmotorized recreation rights are retained, essentially keeping this area as natural habitat.

The Twinings developed the following restrictions on the land to ensure their vision. Overall, commercial uses not derived from, or compatible with, maintaining oak woodlands are not allowed. Roads are to be constructed using the Resource Conservation District's Best Management Practices. Activities that pollute water are prohibited. Manipulation of watercourses, except for habitat restoration or conservation, is not permitted. Within the Oak Woodland Zone, there may be no residential nor other building, and the impact of grazing is controlled by Residual Dry Matter requirements. We are also exploring another approach to ensure that overgrazing does not occur—stubble height limitations.

The management of the woodlands has several goals. The first is to manage the lands to maintain the native forest types on the ranches, especially the blue and oracle oak woodlands. There is a maximum commercial harvest of three cords of wood per year, as the Twinings did not want firewood harvest to ever be a motivation to cut the trees. In addition, they allowed trees to be cut for disease control, fire prevention, personal safety, and salvage after a catastrophe. Non-commercial vegetation management is also permitted.

The easement created considerable value and compensation to the Twinings in tax benefits, in addition to the comfort of seeing their vision ensured. Using a third party appraiser, the unrestricted value of the ranches before the conservation easement was $3,100,000. Under the appraisal with the conservation easement restrictions, the value was reduced to $1,250,000. Thus, the conservation easement value is $1,850,000, or 60 percent of the entire value. Doing what they wanted to do, and benefiting the public with conservation, gained the Twinings a 60 percent reduction of taxable value.

Government Programs that Partner with Private Institutions

In addition, the Twining's costs were largely paid for by a new government program, the California Forest Legacy Program, which was signed into law in 2000. Created initially in the 1990 federal Farm Bill, this is a new state program really designed to help private landowners who manage sustainably to stay in business. The California Forest Legacy Program provides funding for acquisition of conservation easements on private productive forestlands. Its goal is to prevent forest and woodland conversion and to protect wildlife habitat, biodiversity, watersheds, fisheries, natural ecosystem functions, and long-term sustainable uses. The California Department of Forestry and Fire Protection is doing an excellent job building the program with the USDA Forest Service.

Another significant new public program is the California Natural Heritage Preservation Tax Credit Act. Under this program, $100 million is available in state tax credits for donations of qualified lands and water for permanent preservation. This is a big incentive for the donation of a conservation easement, as this allows a tax credit of 55 percent of the contribution value, to make up the difference between the tax deduction and its gift value. However, it does require a public hearing for approval of the donation, which other transactions do not. This is another excellent tool for landowners with whom you work to consider.

Private Conservation Markets

These are some examples of a growing public conservation market and public and private institutions to help implement it. What about private markets for conservation? This is the holy grail of conservationists—to harness the power of private capital to promote and benefit ecosystem health. Well, I suggest there are some real market possibilities relating to carbon storage or sequestration by forest ecosystems. By reducing emissions of carbon dioxide, the primary greenhouse gas, forests can help mitigate the risks of global warming. However, no market exists in a vacuum. Buyers need a reason to buy and sellers need a reason to sell. The carbon market has evolved out of the 1992 Earth Summit in Rio de Janeiro. That created a global partnership for economic progress and environmental protection under the United Nations Framework Convention on Climate Change (UNFCCC). The goal is to stabilize greenhouse gasses to sustainable levels and, to date, is the most complex, far-reaching international treaty ever created.

After a series of meetings following the Rio Summit in 1997, the Kyoto Protocol was proposed to implement the UNFCCC. The Protocol was to reduce greenhouse gasses, especially committing developed countries to reductions in carbon dioxide emissions. The Protocol is not in force; the US has signed but not ratified it. Starting in 1999, negotiations began to determine how to implement the Protocol. The negotiations in November 2000, the so-called Sixth Conference of the parties to UNFCCC, were continued into July and October 2001 as countries continued to discuss modalities of implementation. For the U.S., it is very difficult to see implementation without new rules as the Senate, essential for treaty ratification, passed the "Byrd/Hagel" Amendment (sponsored by Senators Byrd and Hagel) 98-0, which states that there will not be ratification until: 1) costs are "feasible;" and 2) developing countries like China, which have very rapidly rising carbon dioxide emissions, join. Then, in the summer of 2001, the Administration withdrew from Protocol negotiations.

Thus, while the Protocol is unlikely to be realized in anything like its current form in the United States, its substance is likely to be used again. This includes a number of Protocol Articles which concern forests: Article 2, which states the importance of forests; Article 3, which concerns forests and direct domestic reductions; Article 6, which concerns both intersectoral and intercountry carbon trading; Article 4, concerning Joint Implementation; and Articles 12 and 16, which concern the Clean Development Mechanism.

These Articles underscore the importance of forests not only as "carbon sinks," but also as carbon sources. Forests are the second largest source of carbon dioxide emissions globally as a result of forest conversion and degradation. Sixty thousand acres of forest per year, with concomitant carbon dioxide emissions, are lost in California alone. Forests store carbon as they grow, and emit carbon dioxide when disturbed. So, if you prevent oak woodland and other forest loss and conversion, you prevent carbon dioxide emissions and continue to store carbon dioxide. How much carbon can oak woodlands store? This will vary depending on stocking and conditions. Stores can range from 8 to 40 tons of carbon (24 to 120 tons of carbon dioxide) per acre for forests with 40 to 100 percent canopy.

Depending on the price of carbon, this represents potential income to landowners who conserve forests. These values, at $20 per ton of carbon, can pay for the per acre value of a conservation easement. Thus, a forest carbon market provides private financial incentives to reduce forest emissions, undertake conservation measures, and promote sustainable forestland use and economies. So, effectively, a forest carbon market could provide potentially ongoing incremental payments to landowners for conservation and for sustaining their lands. The Pacific Forest Trust completed the first transaction of this nature last year. We sold carbon credits to help acquire a conservation easement on managed forestland in California.

Why a conservation easement? It is an existing legal tool; we know how to use it; and it ensures monitoring and reporting. Conservation easements put restrictions on land use. The carbon market is a good source of private capital as it pays to sequester carbon and reduce forest emissions. Thus, it pays landowners to keep forest as forest and pays to increase the average age of forest. In essence, the carbon market helps pay for conservation.

While very small today, the carbon market is likely to grow because of legislation driven by concern over global warming and air pollution. This will help create the legal framework for the market. As any new market, the carbon market does not like risk. Legislation is needed to help the new market work by establishing "rules of the game." Bills are being introduced at both the state and federal levels. At the federal level, these bills are coming through many committees, especially the Environment and Public Works, Agriculture, and Commerce committees. The State of California is also taking a lead here, where we have a voluntary Carbon Registry, signed into law in 2000. Internationally, the Bush Administration continues to have a presence at the Kyoto Protocol negotiations, though not officially. Further, this Administration has clearly signaled its intent to use sequestration as a primary tool to facilitate carbon dioxide reductions.

The "carbon market" is an emerging market. There are, to date, only a few pilot projects that businesses are sponsoring. These include Green Mountain Energy Company's landmark project with PFT to prevent and reduce forest carbon dioxide emissions in California. PFT is also establishing regional forest "carbon banks," such as the one we are developing in the Wallowa region in Oregon. A third example is the Illinova project (not PFT) with the U.S. Fish and Wildlife Service which is restoring and preserving bottomland hardwoods along the Mississippi River. A similar project could be undertaken in California to restore our riparian gallery forests. At settlement, California had 45 million acres of forest—and some of the best in the world for carbon stocks. While we will not get all of that back, reforestation for carbon can help us restore many forests and conserve what we still have.

Conclusions

In conclusion, while we are in a very challenging and potentially extremely depressing time for oaks in California, we are also in a tremendously exciting time. The tide of public concern and political understanding of the unacceptability of environmental degradation can and should continue to rise. We have opportunities to build new markets for conservation. We have to think differently about how we create economic value for conservation, and work with new partners, integrating and harnessing economies to promote conservation.

Population experts talk about the world population cresting in 2050. We can envision a world 50 years from now if we do not act, and it is not a pretty picture. However, knowing that we can see a light at the end of the tunnel, that we can see a time when resource pressures from population growth will diminish, we can also plan a very different future for 50 years from now—one where we pay for what we truly value and need, such as a healthy, beautiful place to live based on native, diverse ecosystems. And, with help from people such as yourselves, I look forward to a future where we all benefit from doing the right thing, for ourselves, and for coming generations.

Thank you very much.

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The Importance of Federal Grazing Allotments to Central Sierran Oak Woodland Permittees: A First Approximation[1]

Adriana Sulak[2] and Lynn Huntsinger[2]

Abstract

The interlinkage of privately owned foothill oak woodlands and federal grazing permits in the central Sierra Nevada is examined. Knowledge of the viability of the range livestock industry is important to large-scale conservation of hardwood rangelands in the Sierran foothills. Because ranches in the Sierra often use USDA Forest Service grazing allotments, efforts at land conservation may be influenced by Forest Service grazing decisions. We conducted in-depth interviews with Sierra foothill ranchers with federal grazing permits, asking what they would do if their allowable forage use was reduced. We found that replacing the lost forage with other leased lands is the most common solution anticipated by ranchers. Reducing the size of the herd is another strategy ranchers were willing to consider. Diversification and quitting ranching were the least popular coping mechanisms, and selling the ranch was in between. Decision-makers and conservation groups must take these strategies and the problems they pose into account when developing programs for private ranchlands. As it was found that almost all ranchers in the study leased some of the land they used, the continued availability of leased land, public and private, is likely to be a factor in the sustainability of central Sierran ranches.

Introduction

Statewide, ranchers own about 37 percent of the private land in California, about seven and a half million hectares of grasslands, woodlands, and shrublands (Forero and others 1992). Around 70 percent of the oak woodlands of California are grazed by livestock (Huntsinger and Hopkinson 1996). Much of this land is worth far more as residential development or vineyards than as grazing land. Recently, conservation and stewardship groups have become interested in incentive-based programs for conservation of these lands in the low-intensity agricultural use of ranching. Incentive-based programs for private rangeland conservation hinge on the ability of the owners of these lands to continue to support themselves, and their degree of motivation to remain in ranching. The California Cattlemen's Association, The California Rangeland Trust, and the Sierra Nevada Alliance jointly sponsored this research out of a common interest in the future of ranchland and working ranches in the western Sierra foothills, one of the fastest-growing regions in the State (Duane

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[1] An abbreviated version of this paper was presented at the Fifth Symposium on Oak Woodlands: Oaks in California's Changing Landscape, October 22-25, 2001, San Diego, California.

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1996, Ewing and others 1988). The sponsors feel that with fewer and fewer large working ranches left in the Sierra foothills, and thus fewer large tracts of undeveloped open space, identifying the factors that affect the sustainability of these ranches and the woodlands they use is important. This study focuses on the potential interlinkage between use of publicly owned summer range and ranch sustainability.

While large public tracts exist in the State's forests and deserts, other vegetation types, like oak woodlands and annual grasslands, are predominantly in private hands, part of income-producing or speculative enterprises (Ewing and others 1988). Because ranching demands use of extensive acreages, ranches tend to be large compared to farms and residential properties. Collectively and locally, then, the land-use decisions that ranchers make have large-scale effects on the landscape. Unfortunately, there are many threats to working ranches and the open ranges that they support. Previous work has identified estate taxes, heirship issues, increasing property taxes, the marginal status of the range livestock industry, conflicts with urban neighbors, and fragmentation of grazing lands as pressures affecting ranch sustainability in California's grasslands and woodlands (Hargreave 1993, Johnson 1998, Liffmann and others 2000). One less well-understood, but potentially crucial factor, for a Sierran ranching operation is access to summer forage when oak woodland and annual grassland ranges lose nutritive quality. Many ranchers in the Sierra foothills use USDA Forest Service grazing allotments for this portion of their annual grazing cycle.

Ranchers who use Forest Service montane forage are practicing a pattern of livestock grazing common throughout the pastoral world, and notable in California since the 1850s. "Transhumance" is the herding of animals from the lowlands in winter to the uplands in the summer, as described in the Swiss Alps by Sorre (1950). Changes in elevation correspond to changes in rangeland cover types, each of which is suitable for livestock grazing at different times of the year. In California, winter lowland range is generally valley and foothill grasslands and oak savanna, while the summer uplands are usually mountain meadows. This system allows a rancher to range feed the herd all year round, using the naturalized and native grasses and shrubs. Such use of mountain range in the Sierra predates the establishment of the National Forests in 1906, but was institutionalized and controlled through the granting of summer grazing permits by the Forest Service.

A summer grazing permit specifies a time of year, number of livestock, and often, a system of grazing for the rancher holding the permit, known as the "permittee." Numbers, timing, and duration can be changed by the Forest Service temporarily or permanently as deemed necessary to protect resource values or to meet other demands on the land. Over time, livestock numbers and length of time allowed for grazing on Forest Service lands have declined from peaks reached during the 1920s, and they continue to decline. Studies of western livestock permittees have found ranchers overall to be strongly committed to ranching. Though needing to make sufficient income to continue, they are strongly motivated by lifestyle and the non-monetary benefits of ranching (Gentner 1999, Rowe and others 2001, Tanaka and Gentner 2001).

Methods

The project concentrates on Forest Service grazing permittees of the Tahoe, El Dorado, and Stanislaus National Forests. Participants include ranches in 11 counties in and around the central Sierra foothills and valley, with some owning land or leasing outside the study area. The counties were Sutter, Yuba, Sacramento, San Joaquin, Stanislaus, Tuolumne, Calaveras, Amador, El Dorado, Placer and Nevada counties. The ranchers interviewed had an average head count of 329 (minimum of 64 and a maximum of 880, n=19) and owned an average of 1,731 acres (minimum of one and a maximum of 7,731 acres, n=11). One rancher ran only sheep on the Forest Service allotment, though he did run cattle on private land.

We chose an intensive case study approach using in-depth interviews of permittees and a standardized survey instrument. The project began during the winter of 2000 and is guided by an advisory committee, including representatives of the study sponsors, other conservation organizations, University of California Cooperative Extension, experts in economics, and conductors of related previous research. Surveys were pretested and then reviewed by the study advisory committee and other experts before they were administered. The interviews generally took two to three hours and a written portion was left behind to be filled out and sent back to us. Some topics and questions were developed to correlate with a similar recent study in the Rocky Mountains by E. Tom Bartlett and Helen Rowe at Colorado State University (Rowe and others 2001). The results reported here are responses to three questions adapted, with a few alterations, from the study done by Bartlett and Rowe.

All three targeted Forests supplied lists of their permittees, creating a master list of 60 ranchers. During the end of the summer and fall 2000, 25 interviews were initiated and 19 written portions returned (83 percent of the 23 valid and completed interviews). The questions analyzed here are all from the written portion of the survey so the total responses are 19, about a third of all the permittees in the study area and representative of permittees in this region. Response numbers can be smaller than 19 for some questions because a few participants opted not to answer particular questions.

Results

The first question we review here asked participants to rate how important different reasons for using the Forest Service allotment were to them. The next question asked the permittee to choose the strategy he would implement to compensate for a reduction in forage by the Forest Service of 25 percent, 50 percent and 100 percent. A related question asked the participant to outline in more detail the strategies envisioned for each reduction level. The third question asked ranchers directly about the likelihood of selling their ranch. Finally, respondents were asked about the financial consequences the participant expected to experience due to changes in federal allotment access.

The summertime availability of Forest Service range with high elevation green forage proved an important motivation for ranchers for using their allotments. Almost all, 95 percent, of permittees rated green feed “more important” and “ highly important” as a reason for using their Forest Service allotment *(table 1)*. The cost or lack of alternatives, economic sense, and lifestyle were rated as more or highly important by a strong majority of respondents. Convenience was rated as more or highly important by nearly two-thirds of the respondents, while nearly two-thirds of respondents rated the tradition associated with going to the mountains as not important.

Table 1—*Permittee responses to the question, "How important to you are the following reasons for using your central Sierran Forest Service allotment(s)?" in 1999.*

n=8	**Not or somewhat important**	**More or highly important**
Green feed (n=17)	1 (6 pct)	16 (95 pct)
Cost of alternatives is higher (n=17)	2 (12 pct)	15 (88 pct)
Lack of another alternative (n=18)	3 (17 pct)	15 (83 pct)
Makes most economic sense in your current situation (n=18)	2 (11 pct)	16 (89 pct)
Lifestyle: the pleasure of ranching at higher elevations (n=18)	2 (12 pct)	16 (88 pct)
Convenience (n=19)	7 (37 pct)	12 (63 pct)
Tradition, previous owners used the permit before you (n=14)	9 (64 pct)	5 (36 pct)

Ranchers were asked to choose possible compensation strategies for different reduction levels in Forest Service forage. The exact question asked was: "If the Bureau of Land Management or the US Forest Service were to permanently decrease the allowable forage by either 25 percent, 50 percent, or 100 percent on your permit(s), what would be your most likely response or responses?" We allowed respondents to circle more than one response for each reduction level.

The response choices were:

1. *Continue* ranching without change = You can continue your current operation without change.
2. *Sell* your ranch = You would sell all or part of your ranch. You might leave ranching altogether or buy a ranch elsewhere.
3. *Stop* ranching = You would hold on to the ranch but stop ranching. You might lease the ranch out to someone else.
4. *Reduce* production = You would cut back on livestock production, reducing your herd.
5. *Replace* federal forage with other forages = You would replace public forage loss with other forage sources, avoiding any reduction.
6. *Diversify* ranch production = You would diversify your ranch operation.
7. *Employment* off ranch = You would supplement your income by pursuing more or better paid off-ranch employment.

Most ranchers chose reductions in production and replacement of forage as the most popular solutions for all the different reduction levels *(fig. 1)*. With a 25 percent reduction many felt they could continue their business as they do now. One point to note is that selling the ranch, while not the most popular solution for any reduction level, gains in importance as the reductions increase in severity. Additionally, selling the ranch is always more popular than diversification. More than a third of respondents marked selling the ranch as a strategy if the Forest Service reduced their grazing completely. Nevertheless, a majority indicated they would attempt to replace the forage or reduce the herd at the 100 percent Forest Service reduction level.

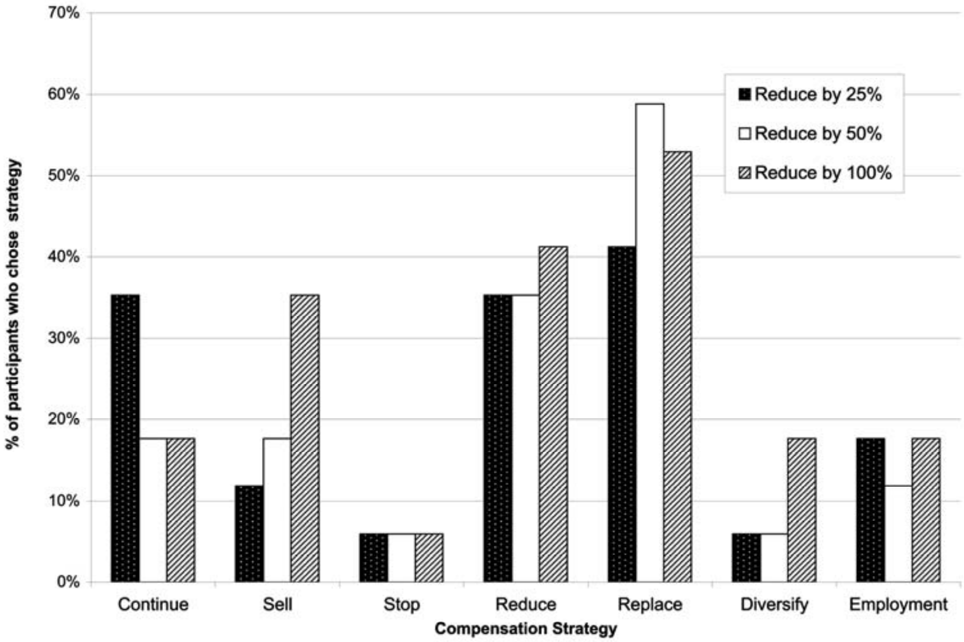

Figure 1—Compensation strategies central Sierra ranchers say they would choose if their Forest Service grazing allotment were reduced by 25, 50, or 100 pct (n=19).

Next the participant was asked to describe in more detail the strategies they would use to cope with reductions in permitted grazing. Not all the respondents who answered the first question completed this part, but those that did mostly outlined strategies of forage replacement. Potential plans for finding another allotment or private ground were mentioned, though the difficulty of finding private forage was highlighted in a few cases. Overall the changes resulting from a 25 percent reduction were not severe. The strategies outlined in response to 50 percent and 100 percent reductions were similar, and more severe, which could imply that the 50 percent reduction level might be a threshold after which using the allotment is not so practical for many ranchers.

Balancing the costs of working up in the mountains against the money made from it was brought up as important in the response decision. One participant mentioned that at 25 percent reduction they thought they could still justify the expense of working up on the allotment, and would find replacement forage for the extra animals. Another rancher responded that when using Forest Service summer range, they are not able to supplement their income with off-ranch employment due to the time required to work the cattle in the mountains. Consequently, if they continue using the mountain range, potential compensation with off-ranch income is limited.

One respondent discussed diversification options as a possible coping method at the 100 percent reduction level. The rancher listed ideas such as new crops or on-ranch vacation marketing, but also described all the difficulties with those options (insurance, land-use regulations, large initial capital outlay). One participant even mentioned fudging on the numbers on his allotment as a solution at all of the three reduction levels. With a 50 percent reduction, another mentioned that he might be able to sustain the ranch by grazing down the Forest Service range a little farther. A ranch that leases out forage to other ranchers said that it would have to lease out less and less of that land to others as reductions moved from 25 percent to 100 percent on the Forest Service allotment, therefore losing income from the leasing enterprise.

A complication apparent in some of these scenarios is the intermingling of public utility land and private land owned or leased by the rancher using the allotment with the Forest Service allotment land. At the 100 percent reduction level, one respondent mentioned subdividing his own land within the allotment boundaries as a way to gain some income. Another rancher mentioned a private lease associated with the Forest Service range and answered that her response would be dependent on the actions of that landowner. One respondent mentioned selling his land holdings within the allotment boundaries if he faced reductions at the 100 percent level.

We then asked the participants about what types of things they might do on their private land in response to forage reductions on Forest Service permits. One question specifically addressed the strategy of selling the ranch, but there were few responses indicating that this was a desirable outcome *(table 2)*. The majority of the answers indicate that most of these ranchers do not intend to sell their ranch, but are committed to their land and to ranching. Many of the participants chose not to answer the question, so the sample size is much lower.

Table 2—*Likelihood of selling all or part of the ranch in response to grazing reductions on Forest Service allotment, central Sierran permittee, 1999.*

Please indicate the likelihood of using the following strategies on your private land:	Very or somewhat unlikely	More or very likely
Sell the ranch - leave ranching entirely (n=10)	10 (100 pct)	0
Sell the ranch - buy a ranch elsewhere (n=9)	7 (78 pct)	2 (22 pct)
Sell part of the ranch - continue ranching (n=10)	8 (80 pct)	2 (20 pct)
Sell part of the ranch - discontinue ranching (n=9)	9 (100 pct)	0

Finally, permittees were asked "How well do you think your strategies would compensate for public forage loss?" and were given a choice of 3 possible responses *(table 3)*. Within the small group that answered the question, most of these ranchers felt that their strategies to compensate for a loss in Forest Service forage would cause them to have a net loss in income (62.5 percent n=8, *table 3*). It is intriguing that there are a few ranchers who believe they could make more money without the allotment.

Table 3—*How well do you think your strategies would compensate for public forage loss?*

n=8	Number of respondents that chose the option:
I could make more money	2 (25.0 pct)
I would have a net loss of income	5 (62.5 pct)
I would have an initial loss but after a few years I could regain present status	1 (12.5 pct)

Discussion

Economics, a perceived shortage of replacement forage, and lifestyle are all important reasons why ranchers continue to use Forest Service mountain allotments *(table 1)*. The first two of these reasons to graze on Forest Service land, green feed and economics, are reflected in the compensation strategies listed by ranchers as responses to Forest Service grazing reductions.

Replacing Forest Service forage is the most desirable option for permittees if permitted grazing is reduced *(fig. 1)*. If finding alternative forage at a reasonable price proves impossible, then reducing head is the next choice for the permittees in this study. Cessation of ranching and diversification were the least popular strategies to cope with reduced public land grazing. Most important for those interested in conserving open space or ranching is the relative popularity of selling the ranch, especially in comparison to diversifying. While overall, ranchers seemed highly reluctant to consider selling their ranches, most of the participants believe that they would choose to sell the ranch, or part of it, before they would diversify their income sources *(table 2)*. Ranchers in the study indicated that if they were to sell land, they would either sell the whole ranch and move to ranch elsewhere, or sell part of the ranch and continue to ranch.

When respondents described their strategies, replacement was again the most frequently cited solution. Though not addressed in this study, the common assertion by many involved in the local industry is that there is no land left to lease. Most Forest Service permittees do not have enough private land to support their existing herd in both the summer and the winter. Even those that do have enough land reported that if they stopped using the allotment, they would have to take that land out of another enterprise and use it themselves, therefore depriving some other rancher depending on that forage. This kind of a scenario would compound the competition for non-federal leases. Many of the ranchers we spoke with talked of the intense competition already apparent for grazing land. There were stories of lessors being approached annually by ranchers looking for leases and offering to pay more money. All but one of all the permittees in the study leased non-Forest Service land already. In some cases another solution for a loss of forage could be additional feeding of hay or other feeds, though these generally cost more than leased range.

In the summer of 2001 we interviewed ranchers without Forest Service leases, though a few of them had held Forest Service permits in the past. The compensation strategies these ranchers used in response to losing their Forest Service allotment were somewhat similar to those proposed by current permittees. Two ranchers purchased more land, one outside of California. One ranch reported that making this change did not increase costs, though he now shipped cattle out of state, but the other found that increases in hauling and labor meant increased costs. The other ranch that discussed compensation strategies reported that they reduced cattle numbers and felt that their business is better off now because of the change. The decrease in head brought down their costs since they no longer have to lease as much land.

This shows that the most popular compensation strategies anticipated by current permittees have succeeded for some ranches in the past. We did not interview ranches that lost their permits and then went out of business, so we missed that point of view. When we asked non-permittees if they found it difficult to find adequate forage for their cattle, 12 out of 14 felt that it was difficult, no matter what the time of year. At this point we don’t know if there is enough forage available in the central

Sierra to serve the total ranch demand if all permittees were to attempt to replace their summer Forest Service forage.

Conclusions

Ranchers use Forest Service forage because in their opinion it is a financially wise decision and it plays an essential role in their forage supply calendar *(table 1)*. These ranchers believe that using Forest Service forage makes the most economic sense in their situation. Additionally, the allotment affords them the ability to leave the foothill/valley home ranch or lease and go to green feed. The lifestyle associated with living in the mountains during the summer is also popular with permittees *(table 1)*.

Attempting to replace Forest Service forage appears to be the most common solution to reductions in grazing anticipated by this group of permittees *(table 2)*. Replacement would entail two relevant changes: cost and availability. The changes in costs due to altering location, buying feed, purchasing land, and paying a fee for an alternative summer lease are not discussed here. Availability of replacement forage is undocumented for the study area as far as we have discovered, but is commonly assumed to be low. All of the non-permittees we interviewed leased some private lands, and felt it was difficult to find enough. The next most popular solution to reductions in grazing on Forest Service land is reduction in herd size.

Noteworthy for those interested in conserving open space and ranch lands, the option to sell the ranch is not a popular option *(table 2)*. For the most part, the ranchers that are still in business have been weeded out through an attrition process and are likely to have a strong commitment to ranching (Hargreave 1993). As *table 3* indicates, very few of these ranchers believe it is likely that they will sell their ranch. Those that do indicate the possibility of selling are intent on staying in the business, but either think it is likely they will sell some of their land and continue ranching, or sell the whole ranch in the study area and make a go of it elsewhere.

Working ranchers, like those interviewed for this survey, are at risk from many different angles. Reduction in Forest Service grazing is one potential problem. For proponents of ranching in the western foothills and valleys of the Sierra Nevada, these results imply that availability of replacement summer leases is important for the future of ranching in the Sierran foothills. The ranchers we interviewed are highly committed to ranching, and would benefit greatly from a more stable forage availability situation than they face either with the Forest Service or competing for the alternative leases.

Further study might include an analysis of the amount of grazing lands in the study area, their present use, and likely future. What portion of ranchland in these counties is linked to Forest Service grazing allotments is a subject of our ongoing study. Most of the ranchers in this study also had private leases, and we do not know the trajectory of that forage supply. It is possible that some grazing leases are on land being held for speculative real estate purposes, and will go out of grazing use relatively soon. Existing tax incentives mean that those anticipating development in the long term can keep taxes lower by leasing land for grazing and keeping in agricultural use in the meantime. Additionally, a serious look at the feasibility of diversification strategies and a marketing or educational campaign to ranchers might ease the competition for replacement forage while also offsetting lost income.

Acknowledgments

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The Effect of Topography, Vegetation, and Weather on Cattle Distribution at the San Joaquin Experimental Range, California[1]

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Abstract

In this study livestock distribution on the landscape was mapped during two seasons, summer and winter, for two years to determine where livestock congregate and to model factors that influence livestock distribution. Two small herds of cows were observed in separate range units on the San Joaquin Experimental Range for a total of twenty-four 24-hour observation periods to ascertain daily movements and activities. Treatments involving water placement and the use of supplemental feeding sites were implemented to judge the effects of these management techniques on cattle distribution. Animal distribution during daylight hours was determined by videotaping all visible animals in the herd every 15 minutes, then positioning cows on rectified digital orthophotographs. The location of the videographer was determined to an accuracy of one meter using a differential global positioning system (DGPS) to facilitate placement of animals. During nighttime hours, the location of the herd was determined every 15 minutes using the DGPS. Night animal activities were observed using night-vision binoculars and recorded for each time period. Our study identified topographic, vegetative and environmental forces that affected cattle distribution patterns. The effects of these factors varied between seasons and years. Water treatments varied in effect with seasons and size of range unit. They showed little effect in winter when free water was available on the forage. The feeding of supplement also had a variable effect. Animals consumed some supplement at all times, but the amount of supplement consumed varied with supplement placement, as well as with the quantity and quality of available forage. Thermal environment was an important factor in determining cattle location and activity. The social interactions of individual animals were important in determining subgroups that formed the herd units. A probabilistic model was developed from this research and will be tested in future studies.

Introduction

The way an animal uses the landscape is affected by many factors. For domesticated livestock, abiotic factors (i.e., slope and distance from water) and biotic factors (i.e., forage quality and quantity, species composition, plant morphology and canopy cover) act in combination to determine distribution patterns (Senft and others

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1987, Smith 1988). Animals also possess spatial memory that allows them to return to areas with high quality forage (Bailey and others 1996, Laca 1998). Social interactions between individual animals also act to influence animal distribution. Subgroups of animals use different areas of the landscape than other subgroups that form herd units (Howery and others 1996, Roath and Krueger 1982).

The areas that cattle graze without active management and the areas that land managers want them to graze are usually not the same (Bailey and others 1996). For example, riparian zones often receive more use than upland areas because they provide water, shade, thermal cover and a productive source of high quality forage (Ames 1977). Therefore, land managers need tools that can help them modify animal distribution. Two of these tools are the placement of water sources and the use of supplemental feed (Valentine 1990). Off-site water has been used to reduce the time that livestock spend in or near streams (Miner and others 1992). McDougald and others (1989) found that the strategic placement of supplemental feed was effective in reducing grazing in riparian areas during periods when the riparian zone is most attractive. Bailey and others (2001) found that supplemental feed had a zone of influence extending for 600 m from the supplement site.

Bentley and Talbot (1951) developed a range site classification (10 classes) for the San Joaquin Experimental Range (SJER) based on topography, aspect, soils, and tree/shrub cover. This classification reflected differences in animal use as well as forage production. Wagnon (1968) found that cattle grazed swale sites heavily in most seasons. After swales, cattle preferred to graze the gentle slope classes. In winter and spring, animals used predominantly south facing slopes and shifted in late summer and fall to north facing slopes.

The objectives of our study were to 1) map the distribution of livestock in a pasture setting on California foothill rangeland in different seasons, 2) develop a predictive model of animal use, and 3) map changes in distribution in response to management actions (i.e., changing water locations and adding supplement sites).

Methods

Our study used range units 1, 6-2, and 72 on the SJER *(fig. 1)*. Range units 1 and 6-2 were combined into one unit by allowing cattle free access through open gates. The SJER (UTM zone 11N, Easting 257600, Northing 4109300) is located along State Highway 41 approximately 30 km north of Fresno, California. The SJER encompasses 1,837 hectares and has been a research facility since 1934. The SJER is located on the east side of the San Joaquin Valley within the oak savanna vegetation type of the Sierra Nevada foothills. The elevation of the SJER ranges from 213 to 518 m above sea level. Soils are shallow (less than 0.76 m deep), coarse, sandy loams derived from granitic rocks. The Ahwahnee series (Mollic Haplustalf) covers about 96 percent of SJER. The Visalia series (Cumulic Haploxeroll) is found on alluvial or swale sites.

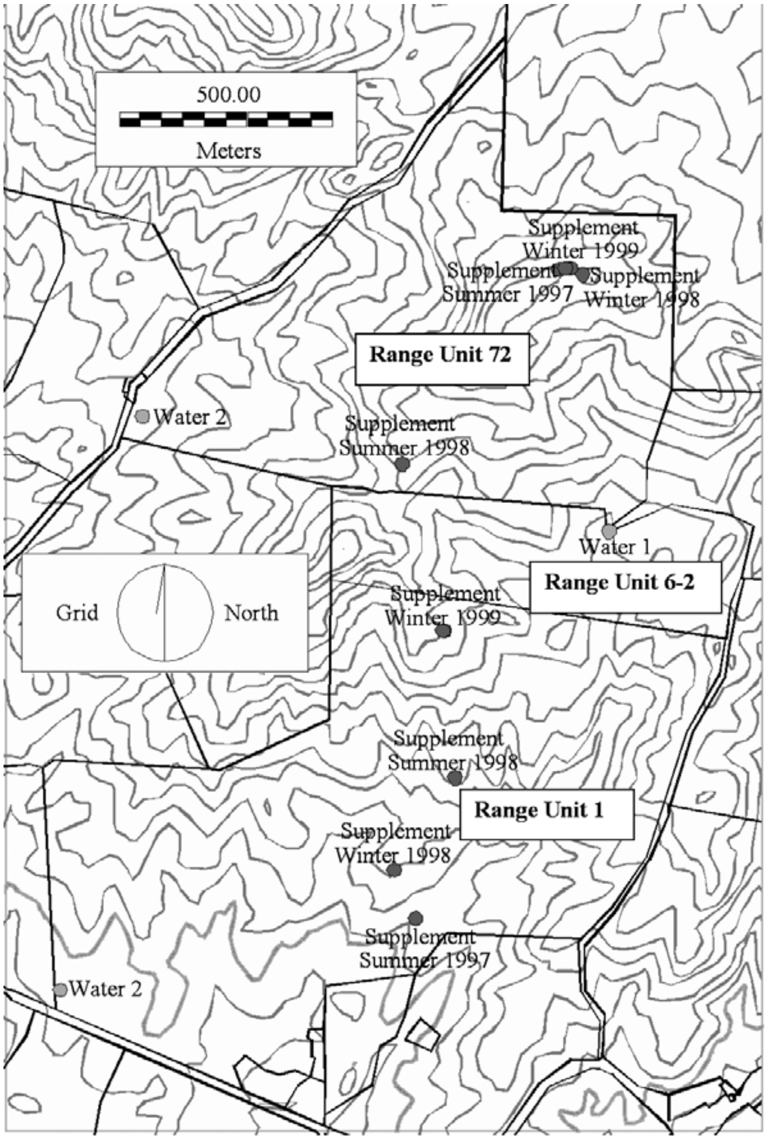

Figure 1—Arrangement of study area showing locations of water and supplement. Contours are 40-foot elevation changes. Fences are shown as broad black lines.

The SJER has a Mediterranean climate. Long-term average annual precipitation (65 years) is 48 cm. However, annual precipitation varies between 23 and 95 cm with most occurring as rain. Snowfall is rare. Rainfall usually occurs between the months of October and March, but may commence earlier in the fall or persist later in the spring. Forage production varies considerably with the amount and timing of precipitation and temperature. Monthly mean air temperature ranges from 6°C in January to 27°C in July.

The annual grasses, soft chess (*Bromus hordeaceus* L.) and foxtail fescue (*Vulpia myuros* [L.] C. Gemlin), and two types of broadleaf filaree (*Erodium* spp.) constitute between 75 and 95 percent of annual herbaceous production. Some of the more productive Visalia soils (approximately 7 percent of the study area) support large populations of bur-clover (*Medicago polymorpha* L.) and Bermuda-grass

(*Cynodon dactylon* [L.] Pers.). The dominant shrubs are two species of ceanothus: wedgeleaf (*Ceanothus cuneatus* [Hook.] T. & G.) and whitethorn (*Ceanothus leucodermis* E. Greene). The evergreen, interior live oak (*Quercus wislizeni* A. DC.), the deciduous, blue oak (*Quercus douglasii* Hook & Arn.) and the conifer, California foothill pine (*Pinus sabiniana* Douglas) compose approximately 98 percent of the tree canopy. Oaks are an important source of shelter for cattle. Trees and shrubs cover about 20 percent of the total surface of the study site.

Standing crop was measured in the middle of each observation series. Forage was sampled at twenty-two locations throughout the two range units. At each location, two 0.093 m^2 (1 ft^2) plots were clipped. Twenty-two plots were also clipped from under the tree canopies located within 10 m of the other sample sites. Vegetation was weighed, dried in an oven at 55° C for 24 hours, and reweighed. Samples were pooled within range sites and canopy locations, ground to pass through a 1 mm screen, and sent to a laboratory for analysis of crude protein and acid-digestible fiber (ADF).

Cattle distribution patterns were mapped using direct observation and videography supplemented by global positioning system (GPS) technology. The timing of observation/treatments was planned to correspond to phenological and physiological stages of the forage referred to in the California literature (Bentley and Talbot 1951, George and others 1996) as the inadequate green (usually October through January) and dry-forage periods (mid-June through September). Supplemental feeding of livestock is common in late dry-forage and inadequate green periods. Observations began in June of 1997 and ended by February 1999. Two teams of observers followed two herds, one in unit 1 and another in unit 72, simultaneously. This approach identified responses to abiotic factors, such as temperature and solar exposure, occurring across units.

Herds of mixed-breed cattle were randomly selected from a large breeding herd of approximately 250 cows. Observation herds usually contained 15 animals and were the only animals in each study range unit. All animals had previously grazed in the study range units, thus were familiar with the parcels. Animals ranged from 2 years to 16 years, with a mean age of 7 years. Ninety-eight different cows were part of the study. Color-coded, reflective tags were attached to their ears to assist in locating animals at night. Bells were placed on two randomly selected cows from each herd to facilitate tracking during night and in dense fog.

Our experiment changed the position of water and supplement in range units 1 and 72 in the pattern shown in *table 1* and *figure 1.* Two existing water troughs in each range unit were selected as water sources; all other water troughs were drained for the study periods. Unit 1 troughs were located 1,657 meters from each other, while unit 72 troughs were 1,120 meters apart *(fig. 1)*. Because water sources were alternated as part of the treatments, float valves were periodically wired shut and troughs were pumped dry *(table 1)*. Similarly, a high protein (20 percent) supplement was placed or removed from each unit *(table 1)*. Supplement sites were located in areas visited by animals but underutilized for grazing purposes. The sites were chosen for each range unit at the start of each series of observations.

Table 1—*Experimental design used for the SJER Cattle Distribution Study. A series of six patterns of water and supplement were presented to animals in each range unit (pasture) during each trial. In the table below, X denotes the treatment was present; a 0 denotes it was absent or unavailable to livestock. See* figure 1 *for position of water and supplement in each pasture for each observation period.*

Observation	Supplement	Water source 1	Water source 2
1	0	X	0
2	X	X	0
3	X	X	X
4	X	0	X
5	0	0	X
6	0	X	0

Two 250-pound barrels of supplement were placed in each range unit. This placement provided one barrel per seven or eight cows. Adequate supplement was maintained during supplemented observation periods. Animals were led to the supplement sites when the barrels were placed in the range units to show them supplement locations. All animals had previously been fed supplement as a normal part of herd operations.

Animals were allowed three to seven days to adjust to treatment changes, then were observed for a 24-hour period. Observers then followed the herds continuously for a 24-hour period. Two types of observations were recorded at 15-minute intervals (scan sampling) depending on whether it was day or night. During daylight hours, observers videotaped all visible animals every 15 minutes to record animal identity, spatial location, and activity. Observers used a Trimble Pathfinder Pro XRS® GPS unit to obtain a positional fix of the videographer.[5] This positional fix, coupled with objects visible in the video and a rectified orthophotograph, allowed individual animals to be accurately mapped on the landscape (± 2m). Videotapes also recorded weather conditions and captured verbal notes from the observers. At night, observers located animals using flashlights and/or night-vision scopes every 15 minutes and obtained a GPS positional fix of their location. Because individual animals could neither be identified nor accurately positioned, herd position was outlined on transparent overlays on an orthophotographic base map. Observers also recorded the total number of animals in the group and the number of animals engaging in each activity (i.e., grazing, walking, laying, standing, drinking, browsing, and eating supplement), air temperature, and weather conditions.

Statistical Analyses

Forage and supplement data were analyzed by analysis of variance (SAS 1998) using two models. Tukey's studentized range tests (SAS 1998) were used to separate means. The model used for analyzing forage parameters included year, season, range site, sampling location (under tree canopy or open exposure) and interactions. Supplement consumption was analyzed using a model that included year, season, temperature, period in range unit and interactions. In both of these models, the residual was used as the error term for statistical tests.

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[5] Mention of trade names or products is for information only and does not imply endorsement by the U.S. Department of Agriculture.

Statistically, the position of cows within a herd or subgroup is autocorrelated because animals tend to move together. Thus, positions of individual animals are not independent observations. This precluded the use of cows as replicates in parametric statistical tests. Analysis of variance was therefore applied to data of only one cow for each observation series. The model used for this analysis included distance from supplement, distance from both water sites, distance from fences, distance from swales, and interactions. As with forage and supplement analysis, the residual was used as the error term.

Stepwise linear regression (SAS 1998) was used to explore and analyze selection of range sites mitigated by forage and time effects. Significance levels to enter and stay in the model were set at P=0.10.

Positional data were expressed as preference indices since each class of independent variables did not contain an equal proportion of the landscape. The preference index was calculated as the ratio of the percentage of total animals observed within a particular class (distance-based or landscape-based) to the percentage of the total accessible landscape within that class (Gillen and others 1984). An index value greater than one indicated that more cattle were observed within a class than would have been expected by random use and was considered to imply positive animal preference for that class. Index values near one are neutral; those less than one indicate avoidance.

Results and Discussion

Our study supported other cattle distribution studies in emphasizing the importance of forage quality and slope as determinants of animal position. Forage quality, as measured by protein and fiber content, *(table 2)* was dependent on season, while forage quantity was dependent on weather factors (amount and timing of precipitation and temperature) throughout the year. The major difference between seasons, winter and summer, was in the crude protein content of forage. Winter levels were significantly (P<0.0001) higher than in the summer, 12.2 ± 1.9 percent versus 6.1 ± 1.4 percent. Forage standing crop differed significantly between years. For summer 1997-winter 1998, the standing crop was significantly (p=0.0001) less than for summer 1998-winter 1999. Standing crop for the first year was 60 percent of the second year's production. During both summers, the forage in the swale sites had significantly more crude protein (P=0.018) than forage on any other range site. However, in 1997 swale vegetation was closely cropped (less than 3 cm stubble height) before the observation series, while in 1998, swale vegetation was over 25 cm in height when the animals were put in the range units. While the protein content (>7.5 percent) of the swale forage was adequate for maintenance, the forage on the uplands was inadequate. Therefore, our observations for summer 1997 occurred during the dry-forage period when the protein content of the forage was inadequate for cattle to maintain weight. Although the forage quality figures did not accurately reflect it, our observations during summer 1998 occurred at the end of the adequate green forage period as a result of a la Niña weather pattern. In the winter, there were no significant forage differences between range sites. In the winter of 1998, the standing crop was 816 kg/ha. Huston and Pinchak (1991) state that, generally, standing grass crops below 1,000 kg/ha restrict forage intake by sheep and cattle on temperate native grasslands of North America. This would indicate that these observations occurred during the inadequate green forage stage. Furthermore, this was reflected in the activities of the cows as they grazed for 12.8 hours a day. In winter 1998, the standing crop was 1,785.5 kg/ha. For all observation periods the cattle preferred to graze swale sites during daylight hours *(table 3)*. A similar pattern was exhibited for all nighttime observations, except for the winter of 1998, when the animals showed a preference for gentle south slopes for nighttime grazing.

Table 2—*Mean forage standing crop and quality available for cattle in each observation series. DM stands for dry matter and ADF stands for acid digestible fiber.*

Observation series	Standing crop kgDM/hectare	Water percent	Crude protein percent	ADF percent
Summer 1997	1690.3	10.1	6.2	50.1
Winter 1998	816.0	77.5	13.4	46.2
Summer 1998	2387.0	16.9	6.1	49.4
Winter 1999	1785.5	74.9	11.1	51.4

Table 3—*Relative preference indices of range sites for grazing during daylight hours.*

Range site	Summer 1997	Summer 1998	Winter 1998	Winter 1999
Swales	5.15	9.68	1.57	3.23
North gentle slope	0.85	0.47	0.72	1.11
South gentle slope	0.64	0.96	1.31	1.03
North open rolling slope	2.33	0.30	1.21	0.19
South open rolling slope	0.97	0.35	1.56	1.01
North brushy rolling slope	0.64	0.16	0.37	0.61
South brushy rolling slope	0.30	0.26	0.53	0.62
North brushy steep slope	0.00	0.00	0.00	0.00
South brushy steep slope	0.97	0.23	0.33	0.79
Steep rocky bluff	1.21	0.03	0.29	0.63

The effect of slope *(table 4)* was also consistent throughout the observation periods, with cows preferring gentle slopes of less than 10 percent. In the winter of 1998, the animals also grazed slopes between 10 and 15 percent. This was a time when very little forage was available, and above average rainfall made the ground in the swales so soft that the animals would sink into it as they walked across.

Table 4—*Relative preference indices of the slope classes for daylight observations only.*

Slope classes Percent slope	Summer 1997	Summer 1998	Winter 1998	Winter 1999	Average
0 to 5	2.9	2.1	1.6	2.3	2.2
5 to 10	1.9	2.5	1.3	1.7	1.9
10 to 15	0.5	0.3	1.5	0.5	0.7
15 to 20	0.6	0.2	0.7	0.7	0.6
20 to 25	0.3	0.3	0.6	0.5	0.4
25 to 30	0.4	0.1	0.6	0.5	0.4
Over 30	0.4	0.3	0.3	0.6	0.4

The effect of water on livestock distribution varied with season. In the winter observations, water was not a factor influencing animal distribution when forage was succulent and covered with dew, or ephemeral streams contained water. In range unit 72, the distance between water sources (1,120 m) was close enough and/or the terrain gentle enough that no water effect was evident in summer observations. In range unit 1, the distance between water sources (1,657 m) was far enough and/ or the terrain rugged enough that a water effect was evident *(table 5)* during summer observations. Water influenced animal distribution for a distance of 900 m in summer observations. The high preference indices for the zone 100 to 400 m from water were biased by the locations of large swales sites and an adjacent shade tree that animals rested under during morning hours.

Table 5—*Relative preference indices for distance-to-water site 1 (range unit 1) when filled with water, for daylight observations only.*

Distance class (m)	Summer 1997	Summer 1998	Winter 1998	Winter 1999	All observations
0 - 100	3.85	8.32	0.96	1.02	3.54
100 - 200	2.62	4.67	0.16	1.72	2.29
200 - 300	3.99	16.38	1.21	3.11	6.17
300 - 400	2.01	3.76	2.01	0.91	2.17
400 - 500	1.38	2.38	4.26	2.53	2.64
500 - 600	1.76	1.56	0.40	1.73	1.37
600 - 700	1.26	1.16	1.33	1.52	1.32
700 - 800	1.93	1.21	1.23	0.73	1.28
800 - 900	1.19	1.36	1.14	1.38	1.27
900 – 1,000	0.99	0.20	1.06	1.16	0.85
1,000 – 1,100	0.96	0.26	0.56	0.33	0.53
1,100 – 1,200	0.38	0.49	0.76	0.30	0.48
1,200 – 1,300	0.74	0.19	1.51	0.96	0.85
1,300 – 1,400	0.10	0.00	0.52	0.00	0.16
1,400 – 1,500	0.00	0.00	0.31	1.10	0.35
1,500 – 1,600	0.00	0.00	0.10	0.54	0.16
1,600 – 1,700	0.00	0.00	0.13	0.13	0.07

Supplement also had a variable effect on animal distribution that was dependent on forage conditions and supplement location *(table 6)*. Animals consumed supplement anytime it was present. However, supplement consumption was higher when the supplement was located close to nighttime bedding grounds. In general, more supplement was consumed during the night than in the daylight hours. In most observations, the zone of influence for supplement was 100 m, but in winter 1998, the zone of influence in unit 72 was 500 m.

Table 6—*Supplement consumption and distances from supplement to water.*

Observation series	Range unit	Supplement consumed kg/animal/day	Distance to water site 1 m	Distance to water site 2 m
Summer 1997	1	0.118	1009.57	844.70
Summer 1997	72	0.748	622.11	1029.03
Winter 1998	1	0.354	936.48	826.69
Winter 1998	72	1.061	603.45	1078.98
Summer 1998	1	0.544	677.73	1045.01
Summer 1998	72	0.839	506.97	616.66
Winter 1999	1	0.680	452.46	1223.24
Winter 1999	72	0.508	622.24	1044.87

The actions of cattle to regulate body temperature are often mentioned in studies as being important in the distribution of animals on the landscape. On sunny summer days, the animals spent considerable time (8 hours) under shade trees near water. During the winter of 1999, the animals would also lay in the shade for a couple of hours on sunny days. However, in the winter of 1998 the cattle exhibited a heat seeking strategy of grazing south slopes during the day and not resting under shade trees. On clear winter days, the cattle would lay down at night on warmer ridges. This was also the pattern they exhibited on the hottest summer days. On rainy winter days, the animals would move to lower, more sheltered areas. During the coldest winter days (–3°C), cattle would move to higher, but still sheltered, areas that were warmer. Supplement was not a strong enough attractant to keep animals on exposed ridges during these times.

Analysis of associations between individual animals showed that the herds were composed of subgroups of animals. These subgroups usually consisted of three to six animals, with groups of five animals most common. Subgroup membership and dominance were age related in our study. Animals of similar ages stayed together, and older animals dominated younger animals.

Conclusion

Our study reached many of the same conclusions as other cattle distribution studies. Three of the factors often cited in the literature as influencing cattle distributions are slope, distance to water, and forage characteristics. Cattle distribution is greatly influenced by slope. Eighty percent of all observations occurred on slopes less than ten percent. In summer, cattle were usually found within 900 m of water. In winter, water was often not a factor. Forage characteristics, quality and quantity, were the single most important factor affecting cattle distribution. Forage in swale areas was high in these characteristics and swales were the preferred landscape site for grazing in all observations.

While many studies have implicated thermoregulation as a factor influencing cattle distribution, this factor is largely undocumented and untested. Our study also implicated thermal environment as being an important factor in cattle distribution. During the hottest part of the day, the cattle were found lying under shade trees. Using solar insolation models, we noted differences between the winter of 1998 and the other three observation periods, indicating that animal were seeking warmer sites that winter. Comparison of our handheld temperature recordings to the USDA Forest Service weather station data indicated that cattle were utilizing warmer ridge tops during clear nights.

We developed a temporal/spatial model of cow movement using the information in this study. Our initial premise is that cattle seek to control their external environment via sensory awareness of the experiences of hunger, thirst, heat, cold, and fatigue, within a social/herding context. At any given moment, an individual will seek to maintain its internal environment by responding to stimuli and by engaging in stereotypic action patterns (grazing, drinking, walking, resting, etc.) at a position on the landscape. Stimuli vary in their intensity throughout the day. This model will be used to generate a probability map for each time period. The accuracy of the modeling technique will be assessed and problems identified. With this procedure, we will gain further insight into cattle behavior and how cattle move and use the landscape.

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Sediment Dynamics and Sources in a Grazed Hardwood Rangeland Watershed[1]

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Abstract

From 1994 to 1998 we documented sediment transport dynamics and sources in a 137 ha grazed hardwood rangeland watershed on granitic soils at the San Joaquin Experimental Range in Madera County. Sediment transport for this watershed was determined by measuring total suspended solids, bedload and flow at an H-flume installed in 1994. Sediment movement as bedload is the primary means of sediment transport in this watershed, with minimal transport of suspended solids. This is attributed to the large sediment particle size and low stream power characteristic of this low gradient intermittent watershed. Bedload transport can be predicted by stream flow ($p<0.0001$, $R^2=0.68$). Upland sediment sources were surveyed using paired hillslope plots to estimate upland erosion for three slope classes. Sediment traps were installed to compare erosion on cattle trails and adjacent non-trailed areas. Ten stream cross section profiles were averaged to determine grazing treatment and year effects on in-stream erosion and deposition along three intermittent stream channels. Due to rapid infiltration, runoff and sediment yield from the hillslope, plots averaged only 151 mm and 36 kg/ha, respectively. Unvegetated, disturbed soil surfaces in cattle trails were a significantly greater ($p<0.002$) source of sediment (0=238 g/trap, n=8 traps) than adjacent well-vegetated soil surfaces (0=6 g/trap, n=8 traps). From 1994 to 1998 stream channel morphological parameters did not change in response to no grazing, winter moderate or concentrated grazing, or dry season moderate or concentrated grazing. There was a year effect on channel depth due to the dynamics of bedload transport in response to variation in peak storm events from year to year. The results of these studies suggest that sediment movement from cattle trails into stream channels is the main grazing-induced sediment source in this watershed.

Introduction

Most of California's surface water flows through the State's 6.8 million ha of annual rangeland. Sediment is the most prevalent non-point source pollutant in these surface waters (State Water Resources Control Board Staff 1999). Causes of erosion within these rangelands include natural processes and historic land use, as well as anthropogenic activities such as road construction and livestock production (Lewis and others 2001). Concerns exist throughout California's Sierra Nevada Mountains

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(Sierra Nevada Ecosystem Project 1996) that livestock grazing increases hill slope and stream channel erosion. Several research and case studies have reported livestock-induced streambank erosion leading to channel down cutting or widening (Hall and Bryant 1995, Kauffman and Krueger 1984, McDonald and others 1991, Sierra Nevada Ecosystem Project 1996). In 1994 we began documenting sediment transport dynamics and sources in a grazed hardwood rangeland watershed on granitic soils at the San Joaquin Experimental Range in Madera County.

Site Description

The 1,752 ha San Joaquin Experimental Range (SJER) in Madera County, Calif. has been a USDA Forest Service research facility since 1935 (Kie 1990). SJER lies in the lower central Sierra Nevada foothills in the oak savanna vegetation type. California State University at Fresno (CSUF) maintains a herd of 210 commercial beef cows at SJER. In 1994 an H-flume was placed at the bottom of a 137 ha watershed that is drained by an intermittent tributary to Cottonwood Creek. Cottonwood Creek is a fourth-order stream that drains into the San Joaquin River just below Friant Dam.

The Station has a Mediterranean climate with annual precipitation ranging from 250 to 800 mm, with a mean of 480 mm, coming almost entirely between October and April. Mean monthly air temperatures range from 6ºC in January to 27ºC in July. Elevation ranges from 213 m to 518 m. Soils are derived from granitic rocks, and most are less than 0.76 m deep. The Ahwahnee series (coarse-loamy, mixed thermic Mollic Haploxeralf) is common, covering about 96 percent of SJER. The Visalia series soils (coarse-loamy, mixed thermic Pachic Haploxeralf) are found on alluvial or swale sites (Ulrich and Stromberg 1962).

Methods

Suspended Sediment, Bedload, and Discharge

Bedload, total suspended solids (TSS), and discharge were determined at a 90 cm H-flume installed at the bottom of a 137 ha. watershed. During the first year TSS was determined from hand collected samples. Beginning in 1995-96, TSS was determined via vacuum filtration through a 0.45 micron filter using water samples collected hourly with an automatic water sampler. Bedload was estimated during four storms in January and February 1998 and 2000. Due to low rainfall in 1999 and 2001, bedload was not measured. Bedload samples were collected using a Helly-Smith bedload sampler (Shen and Julien 1992) to collect three 1-minute samples every hour during a runoff event. Twenty-four means of three hourly samples were plotted against instantaneous discharge to develop a linear model for predicting bedload from discharge.

Upland Runoff

To estimate overland sediment transport within the watershed, three sets of paired runoff plots were constructed using methods similar to those of Singer and others (1980). The three pair were on 10, 20 and 30 percent slopes respectively. The runoff plots and surrounding rangeland were moderately grazed leaving a minimum of 1000 kg/ha of residual dry matter (Clawson and others 1982). Each runoff plot is 2 m wide by 21 m long (parallel to the slope). These runoff plots were established by cutting a 10 cm slit in the ground around the plot and installing 15 cm wide metal flashing. Surface water and sediment leaving each plot was collected and measured after each storm starting with the 1994-95 water year.

Sediment Trap Study

During September 1996, 1997, and 1998 sediment traps (Wells and Wohlgemuth. 1987) were placed in pairs near the first order intermittent stream that drains the research watershed at the San Joaquin Experimental Range. One of each pair was placed in a cattle trail near the point where the trail crosses the stream channel. The second sediment trap of each pair was placed in well-vegetated areas of similar slope and slope length adjacent to the trap in the trail. The sediment traps were emptied as needed or following large storms. Sediment samples were dried and weighed. ANOVA was used to separate treatment and year differences.

Stream Channel Grazing Impacts

Beginning in summer 1994 five grazing treatments were applied to five randomly selected 0.4 ha pastures established for a long-term study along each of three intermittent streams. During this study, streamflow began in early January following 270 to 360 mm of rainfall during October through December. The channels are 0.6 to 3 m wide, 0.3 to 1 m deep, and bedrock-controlled in many reaches. The study reaches are low gradient with less than 2 percent slope and are Rosgen Class B5 (Rosgen 1996). Stream channels 1, 2 and 3 are 2 to 3 kms apart and at an elevation of 274 to 411 m. The treatments were:

- No grazing
- Wet season moderate grazing (stubble height = 5 – 7.5 cm)
- Wet season concentrated grazing (stubble height < 5 cm)
- Dry season moderate grazing (stubble height = 5 – 7.5 cm)
- Dry season concentrated grazing (stubble height < 5 cm)

The livestock concentration treatments were designed to achieve extremely heavy use as is often associated with a feed or watering station. Each grazing treatment was applied to the same pastures in 1994-95, 1995-96, 1996-97, and 1997-98.

Dry season grazing treatments were applied between July 1 and October 1, a period of little or no rainfall. Wet season treatments were applied while the soil was moist and maintained until the end of the growing season. Typically the wet season begins in late October or early November and ends by May 1. This period includes the slow winter growth period and all of the rapid spring growth period of the growing season (George and others 2001). The moderate grazing treatments were stocked at 0.67 ha per animal unit month. Cooked molasses protein supplement and mineral blocks were placed along the streambanks in the pastures treated with the concentrated treatments, and additional animals were added to achieve the target stubble height associated with feeding and watering sites. Instantaneous stock densities equivalent to 250 cows per ha were occasionally achieved but not maintained within the corridor delineated by the cross-section transects.

Stream channel morphological measurements were recorded during the first week of June at the beginning of the dry season starting with a baseline year in June 1994. Channel cross sections were measured using methods outlined by Bauer and Burton (1993). For each stream reach 10 permanent cross-section transects, 6.1 m to 9.1 m long, were placed perpendicular to the stream channel at a distance of 1 to 1.5 times the channel width apart. The transects were marked with permanent stakes and referenced to a permanent benchmark. Stream elevation was determined every 15 cm along the transect using a stretched tape, laser level, and stadia rod. For each transect, width at bankfull, distance from the left permanent stake to right and left bank at bankfull height, depth every 15 cm, and maximum depth were measured. Cross-sectional area, channel average depth, and width-to-depth ratio were calculated. Pasture averages for each morphological parameter were calculated from the 10 transects in each pasture. Cross-section area of the channel was determined using bankfull elevations following the methods of Rosgen (1996). Elevation and position readings of the permanent end stakes were checked with benchmark elevations each year.

Results and Discussion

Suspended Sediment, Bedload, and Discharge

Using hand collected water samples, we estimated total suspended sediment (TSS) delivery from this 137 ha watershed to be 0.18 metric tons per ha during 1995. The NRCS soil loss tolerance value (T factor) for this soil is 5 to 12.5 metric tons per ha per year (Ulrich and Stromberg 1962). The majority of the sediment was transported from the watershed in two storms in January and March. Runoff from the watershed began January 4, 1995 and ended on May 17, 1995. Rainfall for the water year was 773 mm and produced 215 mm of runoff. The rainfall average for SJER is 480 mm. One large runoff event produced an estimated peak flow of 2152 l/sec. During saturated conditions peak flows occur rapidly following rainfall input, then recede quickly when the storm ends. This condition allows for high peak flows that are responsible for most sediment transport in these watersheds. Similar dynamics have been documented at the UC Sierra Foothill Research and Extension Center (Tate and others 1999).

During the first year we observed that most of the sediment was moving as bedload. We began measuring bedload and TSS separately in the 1995-96 water year. Our data indicate that bedload transport can be predicted ($p<0.0001$, $R^2=0.68$) from stream flow where:

$$\text{bedload (g/min)} = 0.0013 * \text{flow (l/min)} + 0.4291$$

Figure 1 is an example of the discharge and TSS data collected since 1995. These results confirm that bedload is the primary means of sediment transport in the watershed, with minimal transport of suspended solids. This is attributed to the low stream power and large sediment particle sizes characteristic of this low gradient watershed. Silt and clay particles are limited in this watershed made up of granitic soils that are 75 percent sand.

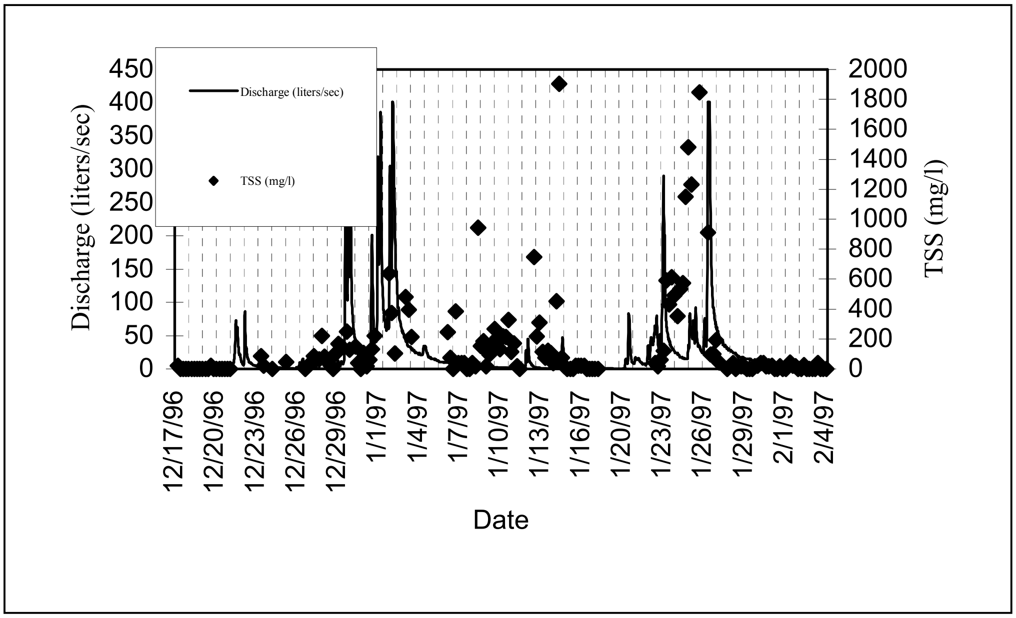

Figure 1—Discharge and total suspended sediment for a small watershed at the San Joaquin Experimental Range in 1995-96.

Upland Runoff

The infiltration rate on these granitic soils is rapid, resulting in little surface runoff or erosion *(table 1)*. While surface runoff is low, water reaches the collection system rapidly during storm events. This suggests that rapid lateral subsurface flow through the soil matrix and via macropores is the dominant flow path from the uplands to the stream channel. We suspect that much of the runoff measured at the runoff plots is subsurface flow from up slope. This was particularly evident in March 1995 when the lowest gradient runoff plots generated the greatest amount of water *(table 1)*.

Table 1—*Monthly runoff and sediment yield hill slope runoff plots for 1994-95.*

Slope (pct)	Jan	Feb	Mar	Total
		Runoff (mm)		
10	0.75	0	225	225.75
20	2	0	90	92
30	15	0	120	135
		Sediment yield (kg/ha)		
10	2.25	.225	16.1	18.6
20	5.84	.337	20.9	27.1
30	27	.562	33.7	61.2

Sediment Trap Study

Sediment transport was significantly greater in cattle trails than in vegetated areas in the rainfall years ending in 1997 and 1998 *(fig. 2)*. There was no significant difference in 1999. In 1997 and 1998 there was sufficient rainfall to generate measurable runoff and the intermittent streams began flowing in January of those two rainfall years. Rainfall in 1998-99 was low, resulting in little runoff and sediment movement in cattle trails. While cattle trail crossings affect a very small total of the channel length within the watershed, the results of this study suggest that trails can be an important conduit of sediment from the uplands to the stream channel. Where livestock trailing is extensive, animal distribution practices (Harper and others 1996) that minimize trailing should be implemented to reduce nonpoint sources of sediment.

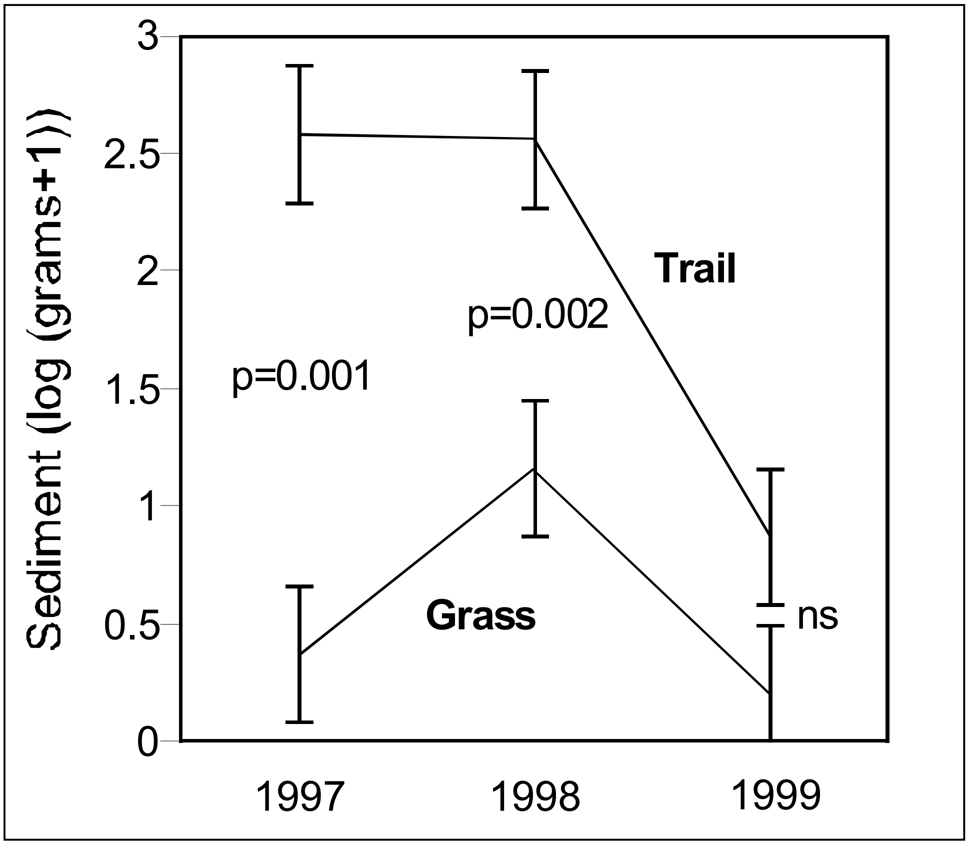

Figure 2—Comparison of sediment trapped in cattle trails and adjacent grass covered slopes.

Grazing Impacts

In 1994 we began estimating the impact of grazing cattle on streambank width and other channel morphology parameters. When stream morphological responses to the five grazing treatments were averaged across all years, no significant difference was detected for either grazing treatment on width, distance to right and left bank, maximum depth, mean depth, cross sectional area, or width-to-depth ratio ($p>0.05$).

There was a strong year effect on stream channel depth ($p<0.05$), reflecting the seasonal and annual movement of bedload along the stream channel bottom.

There have been conflicting reports on the relationship between grazing along stream channels and sediment loss from streambanks (see review by Trimble and Mendel 1996). Several of these studies reported that increased channel width was the result of sloughing of undercut banks. The stream channel banks in this study were not undercut, and could not achieve this form under any grazing scheme due to this substrate type (sand) and dominance by shallow rooted annual vegetation.

We observed grazing and trampling along the stream channel bank by cattle in the treated pastures, yet detected no change in channel width at bankfull. Fine textured and wet streambank soils have been shown to be a factor in vulnerability to erosion (Clary and Webster 1990, Hooke 1979, Marlow and Pogacnik 1985, Marlow and others 1987, Wolman 1959). The well-drained course sands in our study lack the fine particle sizes and have a low water holding capacity that may reduce their vulnerability to streambank erosion. Trimble and Mendel (1995) suggested that watersheds subjected to high intensity, long duration storms generating high stream discharges were more vulnerable to streambank erosion than watersheds that receive relatively equitable flow from snowmelt. During our study one or more high stream discharges occurred each year lasting for only a few hours during and following a storm. Lack of high intensity rainfall and runoff early in the rainy season may reduce streambank erosion. While intense grazing and trampling can leave unvegetated, loose soil at the beginning of the rainy season, low intensity rainfall characteristic of the early rainy season, results in germination and seedling establishment that stabilizes grazed and trampled soil surfaces before periods of more intense rainfall begin.

Summary and Conclusions

In summary we learned the following from this series of studies:

- Bedload is the main mode of sediment transport and TSS inadequately describes channel sediment transport.
- Grazing that leaves adequate residual dry matter in the uplands is not an important source of sediment.
- Cattle trails can be an important conduit for sediment transport from the uplands to the stream channel.
- Cattle grazing as applied in this study does not result in significant streambank erosion when compared to a control or baseline conditions.

To improve our understanding of livestock impacts on rangeland watersheds the results of these studies suggest a need for the following studies:

- Development of the predictive relationship between flow and bedload.
- Estimation of absolute amounts of sediment moving via cattle trails. This will require a study similar to the prediction of bedload from flow, but on a much smaller scale.

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Changes in Soil Quality Due to Grazing and Oak Tree Removal in California Blue Oak Woodlands[1]

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Abstract

The effects of grazing and oak tree removal on soil quality and fertility were examined in a blue oak *(Quercus douglasii)* woodland in the northern Sierra Nevada foothills. Low to moderate grazing intensity has little affect on soil quality; however, oak tree removal resulted in a decrease in most soil quality parameters investigated (carbon, nitrogen, phosphorus, pH) within 5 to 15 years following tree removal. Following tree removal, total C and N pools in the 0-15 cm depth increment decreased by 10 to 20 percent after 5 years and 20 to 40 percent after 21 years. These changes were largest in the 0-5 cm soil depth, but did occur at a slower rate in the 5-15 cm depth. Because all of the soil quality parameters measured are directly related to soil organic matter quantity and/or nutrient cycling processes, removal of oak trees quickly results in a deterioration of soil quality by cutting off the major input of organic matter to the soil. Thus, oak tree removal in blue oak woodland ecosystems in the Sierra Nevada foothills leads to a rapid decline in soil quality and fertility.

Introduction

Oak woodlands dominate the landscape in an estimated 3 million ha in the foothills and Central Valley of California (Griffin 1977) and are used extensively for cattle grazing, providing approximately 75 percent of the forage on California's rangelands. In these oak woodlands, the landscape is a mosaic of trees and patches of open grassland ecosystems. There is great concern about whether regeneration in these oak woodlands is sufficient to sustain present densities (Griffin 1971, 1976; Muick and Bartolome 1987). Rangeland practices, including tree removal to increase forage production and grazing, have been implicated as contributing factors leading to the lack of oak regeneration in these ecosystems.

Total and available soil nutrients have been shown to be higher under the oak canopy than in the surrounding grasslands (Dahlgren and others 1997), and tree removal has been suggested as a way to increase forage production by decreasing the competition for light, water and nutrients. The removal of oak trees has been shown

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to increase forage production 65-650 percent compared to the adjacent open grassland immediately following tree removal (Johnson and others 1959, Kay 1987, Murphy and Crampton 1964). Long-term studies indicate that this benefit lasts less than 2 decades before forage production returns to levels found in the adjacent grasslands (Kay 1987). In previous studies, soils under the oak canopy have been found to contain up to 50 percent more soil organic carbon than soils in the open grasslands. This suggests that oak trees may have a large capacity for sequestration of atmospheric carbon dioxide as soil organic matter; however, this pool of carbon may be quickly released following removal of the trees.

The primary objective of this study was to determine changes in soil quality in response to grazing and as a function of time (5 to 34 years) following blue oak tree removal. Tree removal and grazing are the predominant rangeland practices currently in California, and have the greatest capacity to influence soil quality, ecosystem sustainability, and carbon sequestration.

Materials and Methods

Study Area

The investigation was conducted in the northern Sierra Nevada foothills at the University of California Sierra Foothill Research and Extension Center (SFREC), approximately 30 km east of Marysville, California. The climate is Mediterranean, with cool moist winters and hot dry summers; mean annual precipitation is 73 cm and mean annual temperature is 15°C. The dominant tree species is blue oak *(Quercus douglasii)*, a winter-deciduous oak, with associated interior live oak *(Quercus wislizeni*), an evergreen oak. Major forbs include filaree *(Erodium* sp*.),* annual clovers *(Trifolium* sp*.),* and geranium *(Geranium* sp*.).* Common annual grass species are soft chess *(Bromus hordeaceus),* ripgut brome *(Bromus diandrus),* red brome *(Bromus madritensis* spp*. rubens),* annual fescue *(Vulpia* sp*.),* wild oats *(Avena fatua* and *Avena barbata),* and medusahead *(Taeniantherum caput-medusa)*. The oak understory community has lower species richness and a somewhat different group of plant taxa than the open grasslands (Jackson and others 1990). Soils within the study area formed in basic metavolcanic bedrock (greenstone) and are classified as fine, mixed, active thermic Mollic Haploxeralfs. Slopes within the study area range between 5 and 15 percent.

Four sites were selected in 1999 from grazed rangelands at SFREC in which blue oaks were removed in either 1965, 1978, 1984 or 1994. We also chose four sites within the non-grazed Schubert Natural Area (not grazed in past 28 years) to evaluate the effects of grazing on soil properties. Site characteristics, including soils, vegetation, and topography, were similar between sites. Over the past 28 years, grazing intensity on the grazed sites has remained consistent within the low to moderate range. Cattle are rotated through the grazed portion of the study site for 4-8 weeks per year. At each site *(table 1)*, a composite soil sample (consisting of four subsamples) was collected for the 0-5 cm and 5-15 cm depth increments from four replicates of each experimental condition: (i) beneath an oak canopy, (ii) tree removal sites (identified by stump remains), and (iii) in adjacent grasslands not affected by the oak canopy. For the oak canopy and tree removal sites, soil samples were collected two meters from the tree or stump. For the grazed versus non-grazed comparison, we selected sites from beneath the canopy and from adjacent open grasslands.

Table 1—*Samples were taken at two depths (0-5 cm and 5-15 cm) from grazed and non-grazed sites. Grazed samples were taken from grass, stump and tree areas where trees were removed in 1994, 1984, 1978, and 1965. Non-grazed samples were taken from grass and tree areas.*

Grazed		**Non-grazed**
1994 Tree Stump Grass	1978 Tree Stump Grass	Tree Grass
1984 Tree Stump Grass	1965 Tree Stump Grass	

Analysis

Soil samples for microbial biomass and extractable mineral nitrogen were collected in early May 1999 to coincide with peak standing biomass of the annual grasses. Soil samples for all other analyses were collected in early January 1999 prior to the onset of leaching for the water year. Soil samples were passed through a 2-mm sieve; roots passing through the sieve were removed with a forceps. The <2-mm fraction was split, with one fraction retained at field-moisture content for microbial biomass and extractable mineral nitrogen determinations. The field-moist samples were refrigerated at 3°C until analyses were begun within 24 h. The remaining soil was air-dried at room temperature and used for all other analyses. Bulk density was determined by the quantitative pit method. Bulk density is reported for the <2-mm fraction on a dry-weight basis.

Soil pH was determined in distilled-deionized water and in 0.01 M $CaCl_2$ (1:2, soil:water) following a 15 min equilibration period. Total carbon and nitrogen were determined on ground samples (<250 µm) by dry combustion with a Carlo Erba C/N analyzer. Plant-available phosphorus was estimated using the Bray extraction (1 M NH_4F for 60 s) and the ascorbic acid colorimetric method for PO_4 quantification (Olsen and Sommers 1982). Microbial biomass was determined using the chloroform incubation method (Horwath and others 1994). Microbial biomass nitrogen, mineral N (NH_4^+ and NO_3^-) and potentially mineralizable N were extracted with 2 M KCl. Concentrations of NH_4^+ and NO_3^- in KCl extracts were quantified using a Lachat flow-injection analyzer. In determining potentially mineralizable N, the hot KCl method was utilized with 1 g of soil incubated in 7 ml KCl at 100°C for 4 hours.

Statistical analysis was performed using two-way Analyses of Variance (ANOVA) for all the sites together and one-way ANOVA for each individual site. The two-way ANOVA splits the experimental effects into main effects (are results different for trees, stumps and grasslands?) and site*treatment interaction (is the magnitude of the tree/stump/grassland difference the same at all sites?). A one-way ANOVA was performed on the data stratified by year, along with a post-hoc Fisher's least-significant-difference test to make pair-wise comparisons between treatment means (tree/stumps/grassland) for each site (1965, 1978, 1984 and 1994). The experimental design to examine the effects of grazing was a split-plot; the management regime (grazing versus non-grazed) was the whole-plot treatment factor and the vegetation (oak canopy versus grassland) was the split-plot treatment factor. Tests for the main effects and interactions were performed using ANOVA and a post-hoc Fisher's least-significant-difference test was used for pair-wise comparisons among means. All statistical analyses were performed at a p=0.05 significance level using SYSTAT for Windows, Version 9 (SPSS Inc. 1998).

Result and Discussion

Tree Removal

Total C concentrations were more than twice as high beneath trees as compared to adjacent grasslands, reflecting the "islands of soil fertility" created by the oak trees *(table 2)*. This organic carbon accumulation was rapidly reduced to levels near those of the grassland sites within 5 to 15 years following tree removal. There was a 24 percent loss of organic carbon from the 0-15 cm depth increment over the first five years following tree removal, with 14 Mg/ha lost out of a total of 59 Mg/ha *(table 3)*. Loss of organic carbon appeared to plateau between 30 to 40 Mg/ha after 15 years following tree removal.

Microbial biomass C concentrations were greater beneath the oak canopy as compared to the adjacent grasslands *(table 2)*. Following tree removal, microbial biomass C in the 0-5 cm depth was decreased to levels equal to that of the grassland soils within 5 years. Concentrations appeared to decrease more slowly in the 5-15 cm depth, requiring between 5 to 15 years to decrease to levels equal to that of the grassland soils. Microbial biomass C generally represented between 2 to 4 percent of the total carbon pool and contributed a larger fraction to the grassland soils compared to the tree and stump soils.

Total N concentrations followed a pattern similar to organic carbon with considerably higher concentrations beneath trees as compared to grassland soils and much higher concentrations in the 0-5 cm depth compared to the 5-15 cm depth *(table 2)*. Total N concentrations generally decreased in both the 0-5 and 5-15 cm depth increments following tree removal. A total of 11 percent (0.45 Mg/ha out of a total of 4.0 Mg/ha) of the total nitrogen pool in the 0-15 cm depth was lost from the tree-removal plots five years after tree removal *(table 3)*. Loss of nitrogen reached a maximum value of about 1.2 Mg/ha after 21 years following tree removal.

Microbial biomass N concentrations were generally greater beneath the oak canopy as compared to the adjacent grassland soils *(table 2)*. In contrast to microbial biomass C, the microbial biomass N concentrations did not show a significant decrease at either the 0-5 or 5-15 cm depths five years after tree removal. Microbial biomass N concentrations decreased in the 1965 to 1984 tree-removal sites to levels that were similar to the grassland soils. The microbial biomass N fraction represented from 4 to 8 percent of the total nitrogen pool and did not display any differences between tree, stump and grassland sites.

Potentially mineralizable N (PMN) concentrations were similar in magnitude to microbial biomass N concentrations *(table 2)*. PMN concentrations in the 0-5 cm depth did not decrease in the tree-removal plot in the five years following tree removal, but did decrease to concentrations similar to those of the grassland plots within 15 years after harvest. PMN concentrations in the 5-15 cm depth were highly variable and did not show any strong trends either between treatments or with time since tree removal.

Mineral N concentrations (KCl extractable NH_4^+ and NO_3^-) were about twice as high in the tree plots compared to the grassland plots *(table 2)*. Concentrations decreased rapidly following tree removal and approached levels similar to those in the grassland plots within 5 years of tree removal. In all cases, NH_4^+ was the dominant form of mineral nitrogen. Mineral N concentrations represented approximately 4 to 5 percent of the PMN pool. As with PMN, the concentrations of mineral N in the 5-15 cm depth did not display as clear of a trend as for the 0-5 cm depth.

Table 2—*Mean (± SE) values for selected soil properties comparing the effects of vegetation and tree removal (grass, stump and tree) where trees were removed in 1965, 1978, 1984 and 1994 in a California blue oak woodland. Means in each column within each year (1965, 1978, 1984 and 1994) followed with the same letter are not statistically different at p=0.05.*

		Bulk density (g/cm^3)		**pH**		**Organic C (g/kg)**	
	Depth	0 – 5 cm	5 – 15 cm	0 – 5 cm	5 – 15 cm	0 – 5 cm	5 – 15 cm
1965	Grass	1.14 (0.04) a	1.28 (0.04) a	6.71 (0.09) a	6.40 (0.09) a	35.1 (2.1) a	17.1 (3.4) a
	Stump	1.12 (0.03) a	1.26 (0.03) a	6.53 (0.11) a	6.45 (0.11) a	41.9 (5.9) b	20.7 (3.5) a
	Tree	0.97 (0.04) b	1.19 (0.04) a	7.12 (0.06) b	6.75 (0.11) b	66.4 (11.1) c	35.5 (6.0) b
1978	Grass	1.21 (0.04) a	1.34 (0.03) a	6.32 (0.04) a	6.44 (0.11) a	20.7 (1.5) a	10.7 (1.9) a
	Stump	1.19 (0.03) a	1.34 (0.05) a	6.76 (0.04) b	6.51 (0.02) a	31.8 (1.3) b	13.4 (1.1) a
	Tree	1.09 (0.04) b	1.16 (0.04) b	7.13 (0.03) c	6.69 (0.14) b	57.2 (3.0) c	30.9 (0.9) b
1984	Grass	1.15 (0.03) a	1.29 (0.05) a	6.67 (0.09) a	6.51 (0.09) a	38.0 (5.2) a	10.4 (2.0) a
	Stump	1.14 (0.05) a	1.26 (0.05) a	6.84 (0.09) a	6.67 (0.10) ab	47.9 (4.8) a	13.7 (0.9) a
	Tree	0.99 (0.03) b	1.21 (0.04) a	7.26 (0.07) b	6.81 (0.07) b	68.8 (5.4) b	32.7 (4.0) b
1994	Grass	1.18 (0.02) a	1.33 (0.03) a	6.66 (0.05) a	6.28 (0.10) a	30.6 (4.1) a	6.80 (0.7) a
	Stump	1.09 (0.03) ab	1.29 (0.04) a	7.06 (0.06) b	6.61 (0.04) b	41.4 (1.1) b	17.0 (0.8) b
	Tree	1.05 (0.03) b	1.26 (0.03) a	7.22 (0.11) b	6.62 (0.03) b	50.6 (2.0) b	25.5 (6.2) c

		Organic N (g/kg)		**Microbial C (mg/kg)**		**Microbial N (mg/kg)**	
	Depth	0 – 5 cm	5 – 15 cm	0 – 5 cm	5 – 15 cm	0 – 5 cm	5 – 15 cm
1965	Grass	3.05 (0.19) a	1.45 (0.02) a	782 (22) a	404 (7.5) a	145 (5.4) a	63.7 (5.4) a
	Stump	3.60 (0.53) a	1.56 (0.25) a	755 (10) a	388 (20) a	141 (4.6) a	68.1 (11) a
	Tree	5.05 (0.76) b	2.28 (0.40) b	1507 (300) b	451 (123) a	234 (44) b	84.9 (20) b
1978	Grass	1.80 (0.11) a	0.83 (0.14) a	890 (76) a	262 (26) a	188 (23) a	42.2 (3.9) a
	Stump	2.85 (0.13) b	1.20 (0.03) b	881 (104) a	336 (63) a	205 (15) a	73.5 (9.8) b
	Tree	4.45 (0.29) c	1.90 (0.24) c	1642 (207) b	520 (82) b	284 (44) b	80.4 (4.8) b
1984	Grass	3.75 (0.54) a	1.00 (0.11) a	841 (78) a	218 (15) a	140 (11) a	28.5 (1.7) a
	Stump	4.25 (0.38) a	1.20 (0.05) b	887 (37) a	294 (13) a	152 (7.7) a	52.3 (3.5) b
	Tree	5.18 (0.54) a	1.70 (0.20) c	1338 (43) b	623 (36) b	217 (17) b	99.9 (9.9) c
1994	Grass	2.85 (0.32) a	0.60 (0.03) a	1014 (148) a	252 (36) a	172 (10) a	40.5 (4.0) a
	Stump	3.43 (0.05) a	1.30 (0.08) b	938 (60) a	469 (35) b	203 (14) a	94.4 (16) b
	Tree	3.78 (0.41) a	1.60 (0.50) c	1406 (175) b	678 (40) c	238 (39) a	108 (20) b

		Mineral N (mg/kg)		**Available P (mg/kg)**		**PMN (mg/kg)**	
	Depth	0 – 5 cm	5 – 15 cm	0 – 5 cm	5 – 15 cm	0 – 5 cm	5 – 15 cm
1965	Grass	3.19 (0.30) a	3.19 (1.45) a	2.16 (0.30) a	1.59 (0.20) a	153 (15.5) a	94.9 (9.8) a
	Stump	5.28 (0.80) b	4.37 (0.57) a	3.12 (0.25) a	1.69 (0.30) a	152 (9.2) a	111 (14.1) a
	Tree	12.9 (0.50) c	5.20 (1.10) a	6.15 (0.36) b	2.79 (0.20) b	229 (7.5) b	97.8 (11.2) a
1978	Grass	6.05 (1.30) a	2.07 (0.23) a	1.35 (0.09) a	0.94 (0.12) a	117 (6.4) a	44.2 (9.5) a
	Stump	7.50 (1.80) a	3.74 (0.32) b	2.35 (0.35) a	1.32 (0.10) a	159 (25.0) b	101 (16.4) b
	Tree	13.0 (1.07) b	4.47 (0.40) b	6.47 (0.85) b	3.39 (0.35) b	224 (20.5) c	134 (11.9) b
1984	Grass	4.35 (0.08) a	1.67 (0.10) a	1.67 (0.56) a	1.16 (0.50) a	155 (6.4) a	65.6 (12.1) a
	Stump	7.90 (1.35) a	2.60 (0.25) ab	2.95 (0.60) a	1.32 (0.02) a	191 (25.5) a	81.6 (15.8) a
	Tree	12.0 (1.70) b	4.01 (0.50) b	6.58 (0.90) b	1.93 (0.27) b	244 (25.0) b	93.9 (18.7) a
1994	Grass	5.18 (0.60) a	2.72 (0.36) a	1.94 (0.05) a	0.96 (0.05) a	137 (12.2) a	61.6 (15.3) a
	Stump	7.45 (1.15) a	3.20 (0.40) ab	3.58 (0.60) b	1.35 (0.20) a	202 (18.5) b	89.6 (11.7) a

Table 3—*Carbon and nitrogen pools in 0-15 cm soil depth for tree canopy, stump (tree removal sites) and open grasslands; changes in carbon and nitrogen pools are calculated as a function of tree removal (Loss=Tree–Stump).*

Site	Years since tree removal	Carbon					Nitrogen				
		Grass	Stump	Tree	Loss		Grass	Stump	Tree	Loss	
		Mg/ha	Mg/ha	Mg/ha	Mg/ha	Pct	Mg/ha	Mg/ha	Mg/ha	Mg/ha	Pct
1994	5	27.1	44.5	58.7	14.2	24	2.48	3.55	4.00	0.45	11
1984	15	35.3	44.6	73.6	29.1	40	3.45	3.93	4.62	0.69	15
1978	21	26.9	36.9	67.0	30.1	45	2.20	3.30	4.63	1.33	29
1965	34	41.9	49.5	74.4	24.9	33	3.59	3.98	5.16	1.18	23

Available P concentrations were generally three-fold higher for tree plots compared to grasslands *(table 2)*. Concentrations of available P decreased rapidly following tree removal to levels similar to those in the grassland soils.

Soil pH (water) was generally higher in the tree plots as compared to the grassland plot for the 0-5 cm depth *(table 2)*. The pH of the 0-5 cm depth decreased following tree removal, but the decrease was not observed until more than 5 years after tree removal. In contrast, the pH of the 5-15 cm depth showed a tendency for higher values in the grasslands as compared to the tree plots, and there was no consistent trend resulting from tree removal. Soil pH values measured in $CaCl_2$ were 0.5 to 1 unit lower than those measured in water. The trends for pH($CaCl_2$) were similar to those described for pH (water).

Bulk density of the 0-5 cm depth interval decreased by 0.1 to 0.2 g/cm^3 after 15 years following tree removal. In contrast, the bulk density of the 5-15 cm depth interval was generally the same for all treatments.

Islands of Enhanced Soil Quality

Blue oaks display a striking ability to create islands of enhanced soil quality/fertility beneath their canopy in oak woodlands and savanna. Compared to the adjacent grasslands, soils beneath the oak canopy have a lower bulk density, higher pH, and greater concentrations of organic carbon, microbial biomass C and N, total and mineral N, potentially mineralizable N, and available P. This enhancement of soil fertility is especially pronounced in the 0-5 cm depth and occurs to a lesser extent in the 5-15 cm depth increment.

The ability of the oaks to create islands of enhanced soil quality results primarily from additions of organic matter and nutrient cycling. Blue oaks at the study site returns an average of 9,100 kg/ha/yr of litterfall to the soil surface with its associated nutrients (Dahlgren and others 1997). The added organic matter stores nutrients within its structure (e.g., N, P, S) and also provides nutrient storage capacity in the form of cation exchange capacity. Additionally, canopy throughfall contributes appreciable fluxes of calcium, magnesium, potassium, sulfate and ammonium to the soil surface. Nutrient fluxes in canopy throughfall originate from root uptake and capture of atmospheric aerosols and particulate matter. Because oak roots are found at greater depths (>100 cm) compared to the shallow rooted annual grasses (<50 cm), nutrient uptake by oak roots attenuates leaching losses of nutrients from the soil profile. The extension of oak roots beyond the edge of the canopy may also contribute to nutrient differences between soils beneath the oak canopy and open grasslands. Selective uptake of nutrients by oak roots will deplete the open grasslands of nutrients, while concentrating these nutrients beneath the oak canopy. Further enrichment in the grazed plots may be attributed to shading-up by cattle resulting in some transport of nutrients from open grasslands to soils beneath the oak canopy. Similar mechanisms of nutrient enrichment beneath tree canopies in savanna have been previously proposed (e.g., Belsky and others 1989, Coughenour 1990, Kellman 1979, Weltzin and Vetaas 1992).

A further effect of the oak canopy on nutrient cycling occurs through canopy processes reducing the leaching and erosion potentials (Dahlgren and Singer 1994). Evapotranspiration at the study site is approximately 30 percent greater for the oak canopy plots as compared to the grasslands. This results from greater extraction of water from the soil profile by the deeply rooted oak trees and also due to canopy interception (evaporation of precipitation directly from canopy). This loss of water greatly reduces the leaching intensity beneath the oak canopy as compared to the grassland sites. In addition to the positive effect of organic matter on the soil nutrient status, higher organic matter concentrations lead to lower soil bulk density and greater porosity. This, in turn, provides increased infiltration rates which reduces surface runoff and the loss of nutrients through erosion. Thus, there are several biogeochemical processes by which oak trees concentrate nutrients and create islands of enhanced soil quality beneath their canopy.

Changes in Islands of Soil Quality Following Oak Removal

Changes were evident for all soil quality parameters in the 0-5 cm soil depth within 5 to 15 years. Total C, microbial biomass C, total N, mineral N, and available P concentrations showed a significant decrease within five years. In contrast, microbial biomass N, potentially mineralizable N, and pH values showed a significant decrease within 15 years. We were particularly surprised by how quickly large nutrient pools, such as total C and N, changed following tree removal.

These data indicate that oak trees are capable of sequestering rather large amounts of organic C in the soil profile, and that this carbon is quickly released following tree removal, suggesting that organic matter turnover rates are very rapid in oak woodland ecosystems. Thus, when the litterfall from the oak is eliminated, there is a quick loss of organic carbon as the soil organic matter pool approaches a new steady-state with respect to detrital inputs from the annual grasses. Total litterfall from blue oak at this study site returned an average of 9.1 Mg/ha/yr of organic material (about 4.5 Mg/ha/yr of carbon). This immediate loss of organic matter inputs is quickly reflected in soil organic carbon storage. These data show that oaks may have a large capacity for sequestration of carbon as soil organic matter; however, this pool of carbon is quickly released following removal of the trees.

A similar decrease occurred in the total N pool which has potentially serious ramifications with respect to water quality. Where did this nitrogen go? The two most plausible pathways are losses to denitrification or NO_3^- leaching. In a previous study, Singer and coworkers did not detect any increase in streamwater N concentrations following removal of 14 percent of the trees from the Schubert watershed at SFREC (Singer, personal communication). Furthermore, denitrification rates measured at sites within the SFREC are not sufficient to account for such a large loss of N from the tree removal sites (Davidson and others 1990). We will continue to investigate the potential mechanisms responsible for this loss of N following tree removal.

As with total C and N, the other measured soil quality parameters all respond to tree removal. All of the soil quality parameters measured are directly related to soil organic matter quantity and/or nutrient cycling processes. Microbial biomass is strongly related to the availability of substrate. A large portion of this food source results from the litterfall originating from the oak. Similarly, nutrient recycling is responsible for maintaining available P levels and base cations in the soil surface horizons. The return of base cations to the soil surface appears to increase the pH of the surface horizon. Besides acting as a source of nutrients upon decomposition, soil organic matter also contributes an appreciable quantity of cation exchange capacity that serves as a reservoir for nutrient cations. Thus, removal of the oak tree quickly results in a deterioration of soil quality by cutting off the major input of organic matter to the soil and by breaking a major pathway for the recycling of nutrients to the soil surface.

Grazing

Differences in soil properties between grazed and non-grazed sites were relatively small compared to differences occurring between vegetation types (i.e., oak canopy versus grassland soils) *(table 4)*. In the 0 to 5 cm depth increment, grazing resulted in a slight increase in bulk density, consistent with compaction effects from livestock activity. The increase in bulk density did not extend to the 5-15 cm depth increment. The soil solution pH was approximately 0.2-0.3 units lower in the 0-5 cm depth increment of the grazed soils compared to those in the non-grazed area. Greater nitrification and nitrate leaching and/or export of base cations from the site by livestock may contribute to this apparent decrease in pH. While organic carbon was lower in the 0-5 cm increment of the grazed treatment, it was correspondingly higher in the 5-15 cm depth increment. It is not possible to ascertain whether these differences are the result of natural soil variability or activities associated with grazing. Microbial biomass carbon was higher on the grazed site and may reflect the processing of organic matter by cattle. With a readily mineralizable organic matter source in urine and the high enzyme activity associated with dung, it is likely that cattle excrement stimulates microbial activity. Greater inputs of labile organic matter may increase the availability of substrate for the microbial community, resulting in the higher microbial biomass carbon in the grazed site. The effects of grazing on soil properties were less evident in the 5 to 15 cm depth increment. In contrast, there were large differences in all soil properties between oak canopy and grassland soils throughout the upper 15 cm of the soil profile.

Soils in the grazed area were sampled about six months after the last grazing activity by livestock. We purposely avoided sampling during active livestock grazing to avoid detecting short-term changes that may result from recent grazing activity. Therefore, our sampling was designed to search for longer-term impacts of grazing rather than short-term impacts. Our data suggest that there is no evidence of detrimental effects to the long-term sustainability of the soil quality and nutrient status by low- to moderate-intensity grazing. However, larger impacts would be expected under the more intensive grazing practices utilized on many oak woodland rangelands. Our findings concerning grazing are supported by an analysis of a worldwide data set containing data from 236 sites. This analysis showed no relationship between grazing and several soil properties, including soil organic matter, nitrogen, phosphorus, and pH (Milchunas and Lauenroth 1993).

Table 4—*Mean (± SE) values for selected soil properties comparing the effects of vegetation (oak canopy versus grassland) and grazing (grazed versus non-grazed) in a California blue oak woodland. Means in each row followed with the same letter are not statistically different at p=0.05.*

	Depth	**Grazed**		**Non-grazed**	
	(cm)	**Tree**	**Grass**	**Tree**	**Grass**
Bulk density	0 – 5	1.05 (0.07)ab	1.18 (0.04)c	0.94 (0.06)a	1.08 (0.05) b
(g/cm^3)	5 – 15	1.26 (0.13)a	1.32 (0.11)a	1.27 (0.07)a	1.29 (0.10)a
pH	0 – 5	6.63 (0.14)c	6.09 (0.12)a	6.89 (0.15)d	6.21 (0.15)b
	5 – 15	6.34 (0.19)b	5.87 (0.24)a	6.44 (0.19)b	6.02 (0.13)a
Organic C	0 – 5	59.2 (3.1)b	24.6 (1.9)a	67.1 (7.3)c	25.9 (8.1)a
(g/kg)	5 – 15	26.3 (2.1)c	7.9 (1.2)a	19.7 (4.6)b	9.3 (2.4)a
Organic N	0 – 5	3.9 (0.4)b	2.4 (0.4)a	4.6 (0.9)b	2.9 (0.4)a
(g/kg)	5 – 15	1.6 (0.7)b	0.8 (0.1)a	1.7 (0.7)b	0.9 (0.2)a
Microbial C	0 – 5	1,423 (410)c	1,031 (253)b	1,273 (307)b	737 (241)a
(mg/kg)	5 – 15	657 (80)b	273 (85)a	601 (89)b	329 (128)a
Microbial N	0 – 5	241 (163)b	168 (42)a	217 (41)b	132 (89)a
(mg/kg)	5 – 15	113 (45)b	47 (17)a	91 (32)b	55 (23)a
Mineral N	0 – 5	11.4 (2.3)b	5.4 (2.1)a	18.7 (4.3)c	6.1 (3.8)a
(mg/kg)	5 – 15	4.3 (2.5)b	2.7 (1.8)a	6.6 (2.1)c	2.5 (1.3)a
Available P	0 – 5	6.0 (3.1)b	2.0 (0.6)a	7.7 (2.1)b	2.1 (1.5)a
(mg/kg)	5 – 15	2.9 (1.7)b	0.9 (0.3)a	3.1 (1.8)b	0.7 (0.5)a

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Long-term Residual Dry Matter Mapping for Monitoring California Hardwood Rangelands[1]

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Abstract

Long-term residual dry matter mapping on the San Joaquin Experimental Range provides a working example of this monitoring technique for grazing management and research. Residual dry matter (RDM) is the amount of old plant material left on the ground at the beginning of a new growing season. RDM indicates the previous season's use and can be used to describe the health or condition of annual rangelands. An RDM evaluation is made before the first effective fall rains, usually in late September or early October. Direct clipping and weighing, comparative yields, or photo standards are used to obtain RDM estimates. Mapping of RDM provides a means of recording the total amount of herbage remaining, as well as its distribution on the landscape. RDM is mapped on three different range sites at low, moderate, and high amounts: 1) flat slopes and swales: <400, 600 and >800 lbs/acre; 2) gentle rolling slopes: <600, 800 and >1,000 lbs/acre; and 3) steep slopes: <800, 1,000, and >1,200 lbs/acre. Tracking this information assists management in adjusting stocking rates, selecting locations for livestock supplements and evaluating grazing systems. Researchers can evaluate different grazing impacts on sites, evaluate grazing models, and have a clear understanding of ambient grazing prior to experimentation.

Introduction

Many ranchers and range managers do not fully understand the importance of residual dry matter (RDM) on the California annual grasslands. RDM, sometimes referred to as mulch or plant litter, is the dry plant material on the ground left from previous seasons of growth (Clawson and others 1982, Frost and others 1988, Hedrick 1948). The exact terminology may vary among workers, but RDM consists of three classes or forms: 1) ungrazed mature vegetation still attached to the root system (forage residue), 2) vegetation residues detached from the roots laying on the ground (plant litter), and 3) decomposing residues partially or completely

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incorporated into the soil (humus) (Hedrick 1948, Molinar and others 2001). RDM estimation and mapping for management purposes deals primarily with the first two classes. The rancher's main tool for influencing soil surface conditions is by managing RDM (George and Menke 1996).

Annual plants respond each year to conditions that influence seed germination and early establishment, with fall weather having the greatest impact (Clawson and others 1982). RDM provides favorable microenvironments for early seedling growth, soil protection from erosion, soil organic matter, and it increases water infiltration and soil water holding capacity (Clawson and others 1982, George and Menke 1996, Molinar and others 2001, Rauzi 1960). Plant species composition on annual rangelands is also heavily influenced by RDM. High amounts of RDM favor the development of grass-dominated communities, while low amounts of RDM favor broadleaf-dominated communities (George and Menke 1996). Under normal climatic conditions, adequate amounts of RDM increase forage production on most sites (Bartolome and others 1980, Schwan and others 1949). Furthermore, RDM provides low-moisture fall forage for livestock feed (Clawson and others 1982).

Bentley and Talbot (1951) developed a system of site classification for rangelands typified by the San Joaquin Experimental Range. For the purposes of RDM estimation and mapping, the system consisting of ten site classes can be simplified by grouping sites into three slope categories: swales, open rolling, and steep brushy (Frost and others 1988). For range management, a rapid survey of rangelands can be done using visual estimation and comparative photos. RDM for the sites can be classed into light, medium and high categories using the class descriptions and comparative photos in the U.C. Cooperative Extension Leaflet 21327 (Clawson and others 1982). RDM classes can then be mapped using manual techniques or entered into a geographic information systems (GIS) database.

Mapping RDM periodically through the dry forage period can enhance livestock and rangeland management. RDM maps provide a record of residual dry forage amount and its distribution on a pasture, ranch or allotment. These records assist land managers in adjusting stocking rates (Clawson and others 1982) and selecting locations for water and supplemental feed to better utilize forage (Frost and others 1988). Long-term mapping and livestock use records provide accurate estimates of livestock carrying capacity for rangeland (Frost and others 1988). Researchers can use RDM records to evaluate grazing impacts on sites, evaluate grazing models, and evaluate treatment effects on grazing distribution.

Methods

Long-term mapping of RDM was implemented on the San Joaquin Experimental Range (SJER) in 1985 and is still continuing today. Only the RDM maps from 1985 to 1999 are presented here. The SJER (UTM zone 11N, Easting 257600, Northing 4109300) is located in the Sierra Nevada foothills 28 miles north of Fresno along state highway 41. The SJER *(fig. 1)* encompasses 4,539 acres and has been a USDA Forest Service research facility since 1934. The SJER is within the oak savanna region of the foothills and is characterized by grassy rolling hills with scattered trees and shrubs. Occasionally the stands of trees and shrubs become quite dense. The climate is Mediterranean with mild, rainy winters and hot, dry summers. Long-term average precipitation (65 years) is 19 inches. However, annual precipitation varies between 9 and 37 inches with most occurring as rain. Snowfall is rare at this location.

Rainfall usually occurs between the months of October and March, but may occur earlier or later. Forage production varies considerably with the amount and timing of storm events. Monthly mean air temperature ranges from 43°F in January to 81°F in July. The study site is better described in Bentley and Talbot (1951) or Frost and others (1988).

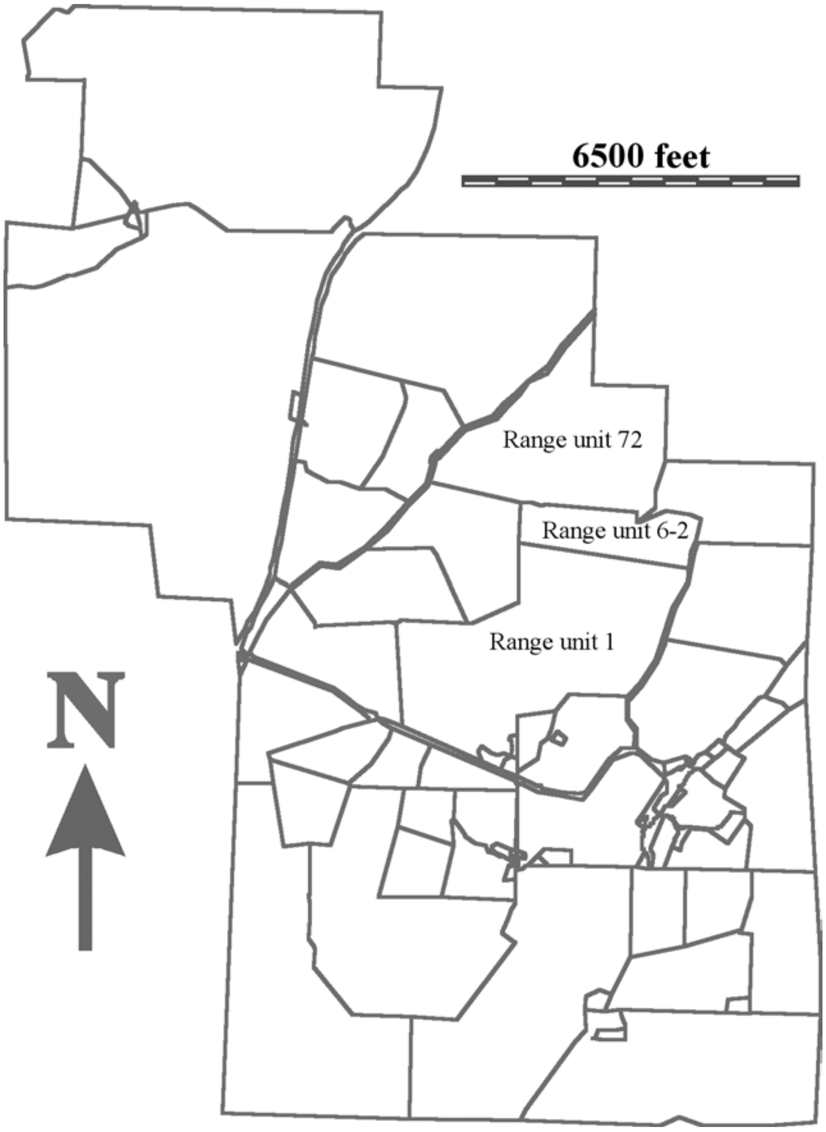

Figure 1—Fences on the San Joaquin Experimental Range showing the locations of range units used for the cattle distribution study.

Livestock management prior to 1995 consisted of rotational management of small groups of cattle through the range units. In 1995, a system of high density-short duration grazing was implemented on the station. Cattle are moved as a large herd unit into each range unit for a short time, one to two weeks, to graze available forage.

RDM evaluation and mapping is made before the first effective fall rains, usually in late September or early October. A double sampling method is used for determining RDM amounts. The double sampling consists of both visual estimation and weight determination. Clipping and weighing a few plots periodically calibrates the visual estimation in the field. Weights are estimated in pounds per acre. The three comparative photos shown in U.C. Cooperative Extension Leaflet 21327 (Clawson and others 1982) are used to provide a consistent reference for delineating RDM classes. The entire station is surveyed in a single day. RDM is mapped on the three different slope classes at low, medium, and high amounts: 1) flat slopes and swales: <400, 400-800, and >800 lbs/acre, 2) gentle slopes: <600, 600-1,000, and >1,000 lbs/acre, and 3) steep slopes: <800, 800-1,200, and >1,200 lbs/acre. An additional class is used to delineate areas burned by wildfires. RDM classes are delineated on a topographical base map using color-codes. The RDM map is then converted to digital format by digitizing it into a GIS database *(fig. 2)*.

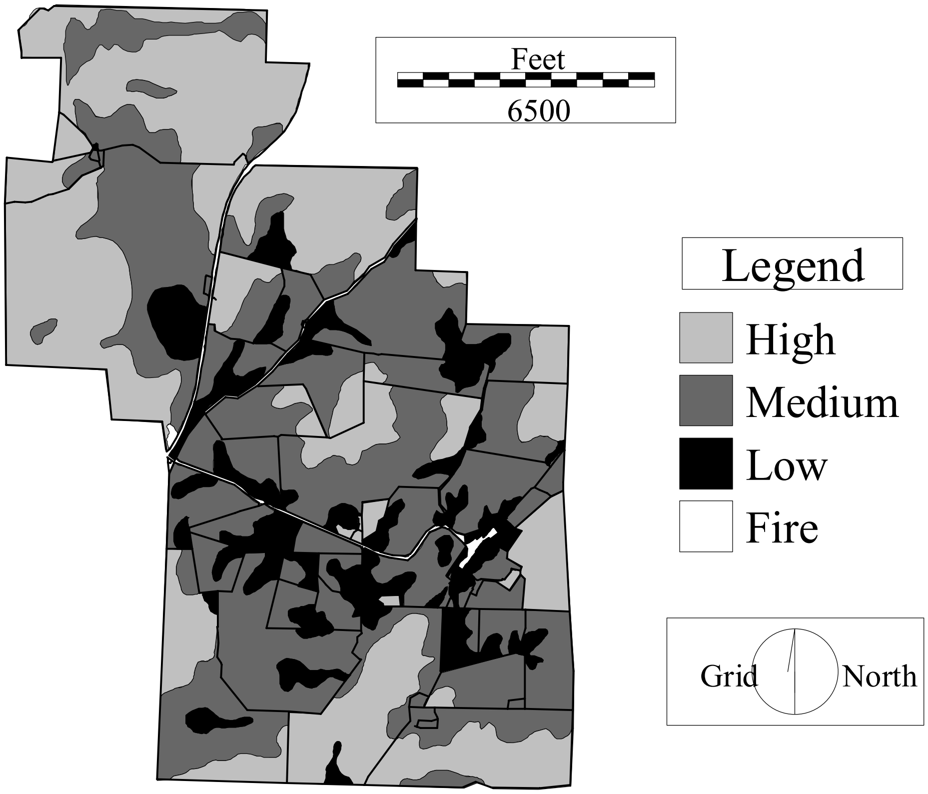

Figure 2—Residue map for 1996 shown with fences.

Direct visual observations were made on two small herds of cattle for 2 years (1997-1998 and 1998-1999), summer and winter. The cattle were observed in range units 1, 6-2, and 72 *(fig. 1)*. For six 24-hour periods, scan sampling observations were made every 15 minutes using video cameras combined with global positioning system (GPS) technology. Observations were mapped spatially and entered into the GIS database. Livestock trails in these units were also mapped using a differentially corrected GPS. These data were used to validate that the RDM spatial patterns were related to animal use patterns.

RDM maps were quantified using the GIS database to calculate the coverage of each RDM class. A composite image of all RDM maps was created using GIS map algebra techniques.

Results and Discussion

RDM mapping proved to be a quick, efficient and accurate method for monitoring livestock use. A team of two people was able to map residue across the entire research facility in one day. The double sampling technique, combined with the comparative photos, provided accurate and consistent results. Calibration clippings at periodic intervals showed estimates to be within 10 percent of actual weights.

In general, RDM mapping revealed the same use pattern for the fifteen-year period. Cattle showed a grazing preference for the swales and shallow, flat slopes. Residue was reduced to medium or low levels before reduction below the high level was detected on the gentle rolling slopes. Reduction of residue on the steep slopes was seldom detected until the residue on the gentle rolling slopes was at the medium level. The other major influence on residue levels was the location of water sources. Areas near water had lower residue weights than areas farther away. Slope and distance to water were the two most cited factors influencing cattle distribution and RDM levels. This was the same use pattern described in Wagnon (1968) and Frost and others (1988). These findings also correspond to conclusions reached in our cattle observation study (Harris 2001). The composite image *(fig. 3)* for the fifteen-year period clearly showed these patterns.

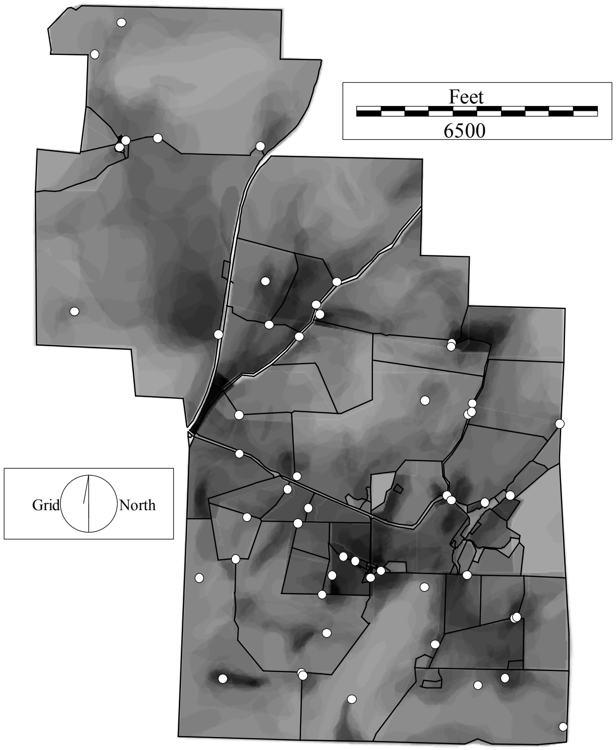

Figure 3—Composite image of 15 years of RDM maps. Light gray shows high residue levels (low animal use) and dark gray shows low residue levels (high animal use). Water sources are shown as white points and fences are in black.

We did not have access to livestock use records and were not able to relate RDM patterns to actual animal use across the SJER. However, for the summer of 1997 we had GIS layers that showed animal distribution for range units 1, 6-2, and 72 *(fig. 4)*. While the total animal use in these range units was not exclusively by the cows in our observations, they were the major influence on the RDM pattern *(fig. 5)*. The two figures showed good agreement between observed animal use and residue levels. An additional influence on RDM levels was shown by the low pattern *(fig. 5)* surrounding the supplement site in range unit 72 (the upper range unit). This low pattern on a ridge was not shown in the previous 12 years of RDM mapping and only occurred in years (1997 and 1998) when supplement was placed on the ridge.

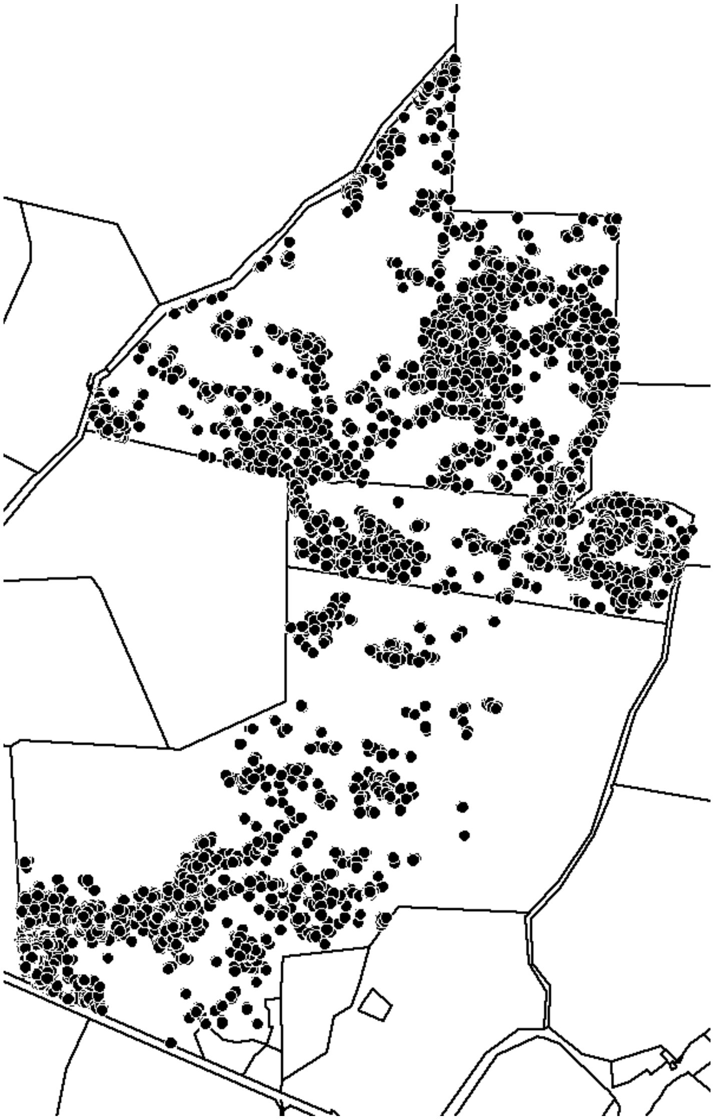

Figure 4—Cattle distribution for the summer of 1997 during daylight hours. Positions show individual cows at fifteen-minute intervals during six observation days.

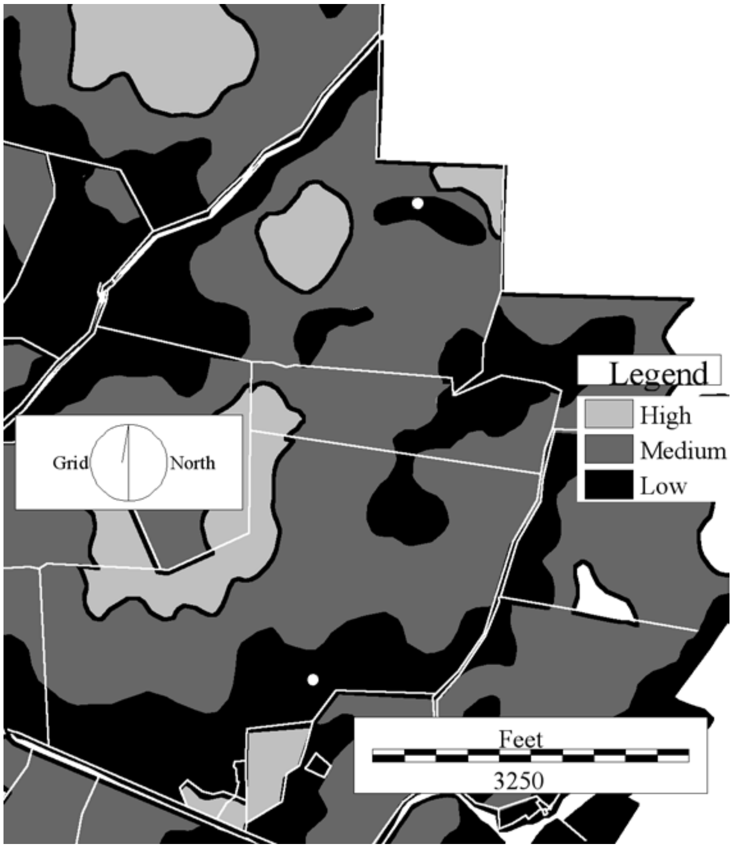

Figure 5—Residue map for range units 1, 6-2, and 72 during the summer of 1997. Supplement sites are shown as white points and fences are shown as white lines.

Livestock trails are the result of animal travel to preferred areas (Walker and Heitschmidt 1986, Ganskopp and others 2000). As such, they are another indicator of animal use. Walker and Heitschmidt (1986) indicate that trail density is a good predictor of animal use, with a high density of trails indicating highly preferred sites. Harris (2001) states that trails proved to identify preferred grazing sites; over 75 percent of all grazing in these range units occurred within 30 meters of a major trail. The trail systems in range units 1, 6-2, and 72 were mapped using DGPS units to within 2 meters. Comparison of the trail systems to the composite image for these range units *(fig. 6)* shows that most trails were associated with areas of lower RDM (darker areas).

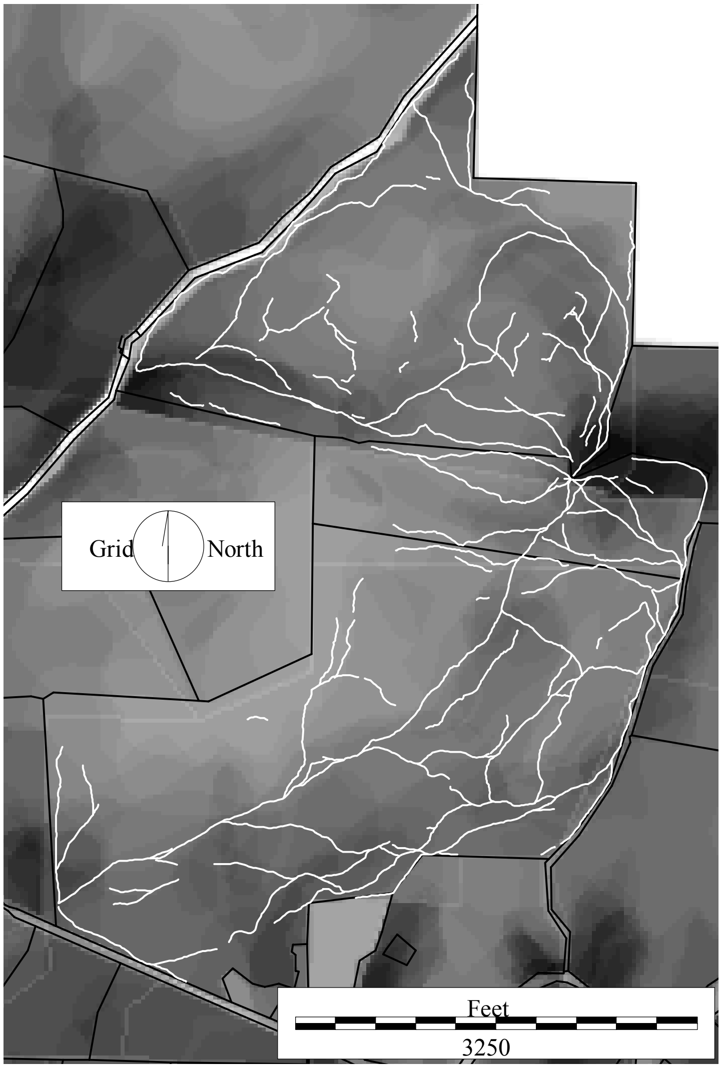

Figure 6—Comparison of composite RDM image (15 years) with livestock trail systems for range unit 1, 6-2, and 72. Light gray shows high residue levels (low animal use) and dark gray shows low residue levels (high animal use). Livestock trails are shown as white lines and fences are in black.

The percentages of area with low, medium and high levels of RDM were not related to forage production and rainfall *(table 1)*. Peak production was the highest in 1992 at 2,699 lbs/acre. This was 468 lbs/acre higher than the 65-year average of 2,261 lbs/acre. High RDM covered 75.5 percent of the area, while low RDM levels covered 2.4 percent. Production was the lowest in 1988 at 807 lbs/acre, or 1454 lbs/acre below the average. Medium RDM covered over half (53.2 percent) of the SJER. High RDM covered 33.6 percent and low RDM covered 13.2 percent of the area. The greatest coverage for high RDM was in 1986 (94.1) when peak production was high (2,653 lbs/acre). The greatest coverage for medium RDM was in 1998 (56.0 percent) and peak production was 2,508 lbs/acre. The greatest coverage for low RDM was in 1990 (40.8) when peak production was far below the average at 845 lbs/acre. Clawson and others (1982) stated that the “moderate” (medium RDM) level of grazing had been recommended for the best livestock performance and range protection in this zone. Using this criterion, the best matches between animal use and forage production occurred in years 1988, 1990, 1997, and 1998 when medium RDM levels were over 50 percent of the area of the station. However, the high percentage of low RDM (40.8 percent) in 1990 might indicate overuse of forage resources for that year.

Table 1—*Percent cover of RDM, peak forage production and annual rainfall for the 15-year period (1985-1999).*

Year	High (percent)	Medium (percent)	Low (percent)	Fire (percent)	Peak production (lbs/ac)	Rainfall (inches)
1985	86.6	11.7	1.3	0.3	1,690	13.6
1986	94.1	4.4	1.5	0.0	2,653	20.8
1987	85.5	6.8	7.7	0.0	968	11.1
1988	33.6	53.2	13.2	0.0	807	12.1
1989	62.8	32.3	4.8	0.0	988	13.0
1990	9.2	50.0	40.8	0.0	845	11.6
1991	78.8	19.4	1.9	0.0	2,338	16.1
1992	75.5	22.1	2.4	0.0	2,699	16.2
1993	76.0	22.8	0.9	0.3	1,829	25.7
1994	51.2	44.6	4.1	0.1	1,328	13.3
1995	64.8	32.4	2.8	0.0	2,355	31.7
1996	39.6	48.4	11.9	0.1	2,651	14.1
1997	28.2	51.5	20.3	0.0	2,286	24.9
1998	30.3	56.0	13.7	0.0	2,508	31.8
1999	33.9	41.0	25.1	0.0	2,191	13.1

Conclusion

RDM mapping can provide an important tool for ranchers and resource managers. It is quickly accomplished and does not require specialized equipment. Mapping of RDM allows managers to identify areas of heavy use and possible erosion sites. Using long-term RDM mapping, prevalent grazing patterns can be identified and sites suggested for water or supplement to modify undesirable use by cattle. Mapping can then aid in evaluating the effectiveness of management actions to correct problems. RDM mapping, combined with livestock use records. assists in evaluating grazing systems and in adjusting stocking rates.

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Seasonal and Site Effects on Oak Fine Root Production and Ectomycorrhizal Colonization in California Oak Woodland[1]

Xiaomei Cheng[2] and Caroline S. Bledsoe[2]

Abstract

At three sites in a blue oak woodland in northeast California, we studied seasonal patterns of blue oak (*Quercus douglasii* Hook and Arn.) fine root (< 2 mm diameter) production and ectomycorrhizal (ECM) colonization using root ingrowth cores. In a short-term study, ingrowth cores were installed and harvested in 3-month intervals for one year. Oak fine root production was lower in fall and winter, higher in spring, and intermediate in summer. ECM roots were found only in spring and fall. In a long-term study, ingrowth cores were installed in January 1998 and harvested after 6, 9, and 12 months, respectively. ECM colonization was higher after the 6-month (winter, spring) interval, lower after the 9-month (winter, spring, summer) interval and intermediate after the 12-month (winter, spring, summer, fall) interval. Both long-term and short-term studies demonstrated that ECM fungi were active in spring and fall seasons. ECM colonization was much higher in an undisturbed six-month interval (winter + spring, long-term study) than in a disturbed 6-month interval (winter + spring, short-term study), suggesting that disturbance decreased mycorrhizal colonization.

Introduction

In northern California blue oak woodlands, plant growth is affected by the typical Mediterranean climate—cool, wet winters and hot, dry summers. Aboveground, oak leaves usually emerge in late March and senesce in October, while annual grasses begin to grow in November after first fall rains and senesce in early May. However, there is little information about belowground root growth. Three studies have quantified the biomass and spatial distribution of oak roots (Callaway and others 1991, Millikin and Bledsoe 1999, Millikin and others 1997), but information about oak fine root production and temporal distribution in California oak woodlands is lacking.

The importance of ectomycorrhizas (ECM) to ecosystem processes has been well documented. However there is little information about the timing of ECM occurrence and the longevity of ECM roots. In a Norway spruce stand in Sweden, there were seasonal effects on ECM formation; the average lifespan of ECM roots was 300-1,000 days, depending on soil characteristics and root branch order (Majdi

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and others 2001). In addition, about 45 percent ECM roots were dead after 200 days (Majdi and Nylund 1996).

In this study, using root ingrowth cores, we measured oak fine root production and ECM colonization at three sites in the Sierra Nevada foothills. The purpose of our study was to examine seasonal effects on oak and grass fine root production and ECM colonization in both short-term and long-term studies. This paper focuses on oak fine root production and ECM colonization; grass root production was reported elsewhere (Cheng and Bledsoe [In press]).

Methods

A short-term and a long-term study were conducted at three sites at the University of California Sierra Foothill Research and Extension Center (near Browns Valley, California) in 1998. For the 4-year period 1996-2000, mean annual temperature was 18°C (summer 24°C, winter 11°C) and mean annual precipitation was 90 cm. In 1998 the temperature was 16°C, while precipitation was 124 cm. In general, precipitation begins in October or November and ends in May. Soils are classified as fine, mixed, thermic Typic Haploxeralfs (Dahlgren and Singer 1991). The dominant trees include winter-deciduous blue oaks *(Quercus douglasii)* and foothill pines *(Pinus sabiniana).* Common annual grasses include *Bromus* spp. and *Avena barbata*. Additional characteristics are found in Cheng and Bledsoe [In press].

The three sites (River, Upland and Hilltop) we selected for this experiment were very similar in vegetation and soil but differed slightly in elevation. At each site, we randomly selected three open-grown blue oak trees. Around each tree, we installed ingrowth cores under the oak canopy and in the open area. Ingrowth cores (40 cm long and 7.5 cm diameter) were made of 3 mm nylon mesh and filled with sieved (2 mm) root-free soil from each site by horizon (A: 0-5 cm; B: 5-40 cm). Before filling cores, soils were lightly moistened with water so that soils remained within the ingrowth cores.

In the short-term study, 18 ingrowth cores (3 sites × 3 trees × 2 replicates) were installed every 3 months beginning in January 1998 and harvested 3 months later. The short-term study lasted one year, thus there were four seasonal sampling periods: winter, spring, summer and fall. In the long-term study, we installed 54 cores in January 1998 and harvested 18 cores after 6, 9, 12 months, respectively. In both studies, oak fine root production and ECM colonization were evaluated.

At harvest, each ingrowth core was removed from the soil and divided into four segments (0-10 cm, 10-20 cm, 20-30 cm and 30-40 cm). In each segment, roots were separated from soil using a root elutriator (Gillison's Variety Fabrication, Inc., Benzonia, MI).[3] Roots were stored in water at 4°C and sorted within one month. Dead oak roots, defined as desiccated, dark brown, shrunken and highly fragile, were separated from live oak fine roots. After sorting, ECM oak root colonization was examined under a dissecting microscope using the grid-line intersect method (Brundrett and others 1996). Colonization was calculated as ECM tips per meter of total root length. Root samples were dried at 70°C and weighed. Fine root production was estimated by measuring new fine root growth into ingrowth cores.

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[3] Mention of trade names or products is for information only and does not imply endorsement by the U.S. Department of Agriculture.

Results

There were no significant differences in oak fine root production between cores located under the canopy and in the open area, so data were combined. At all three sites, seasonal effects were significant *(fig. 1)*. Oak fine root production was lower in fall and winter than in spring. Surprisingly, there was significant oak fine root growth in summer, even though soils were very dry during that time.

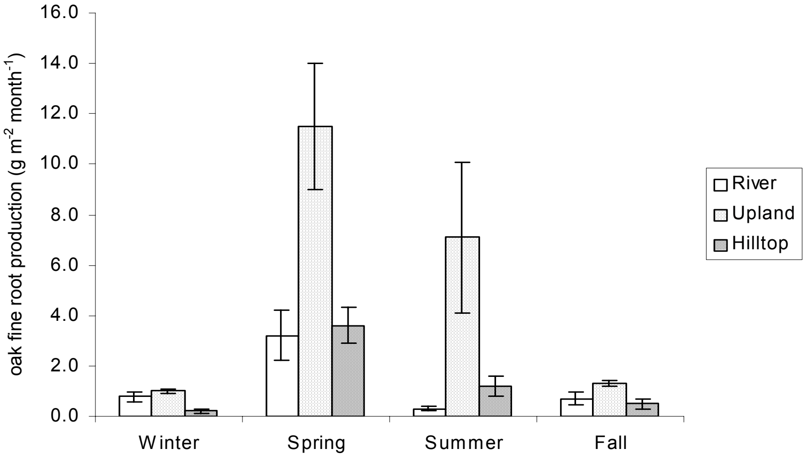

Figure 1—Seasonal effects on oak fine root production at three blue oak woodland sites. Values are means of four to six cores for each season: winter (Jan–Mar 1998), spring (Apr–Jun 1998), summer (Jul–Sep 1998), and fall (Oct–Dec 1998). For each core, data from all four soil depths were combined. Bars are standard errors of means. Data were modified from Cheng and Bledsoe [In press].

Site effects on oak fine root production were also significant. Overall oak fine root production was greater at the Upland site than at the River and Hilltop sites *(fig. 1)*. Annual oak fine root production, which was estimated by adding total root production from each season, was highest at the Upland site (63 g m^{-2} y^{-1}), and less at the River (15 g m^{-2} y^{-1}) and Hilltop (16 g m^{-2} y^{-1}) sites.

Oak fine root production did not differ significantly with soil depth, but did differ with site and season *(fig. 2)*. At the River site, root production was greater in spring than in other seasons at all soil depths (0-40 cm). At the Upland and Hilltop sites, root production was significantly greater in spring than in other seasons in the upper soil (0-20 cm), but was similar in spring and summer in the lower soil depths (20-40 cm).

In both short-term and long-term studies, we examined oak fine roots and determined ECM colonization. No ECM oak roots were found at the Hilltop sites in two studies *(table 1)*. In the short-term study, ECM oak roots were found only in spring and fall. The colonization rates were similar between the River and Upland sites. In the long-term study, ECM roots were found at all time intervals. The colonization rate was higher in 6-month interval (75 and 53 tips/meter, respectively) than in 9-month (21 and 9 tips/meter) and 12-month intervals (42 and 24 tips/meter).

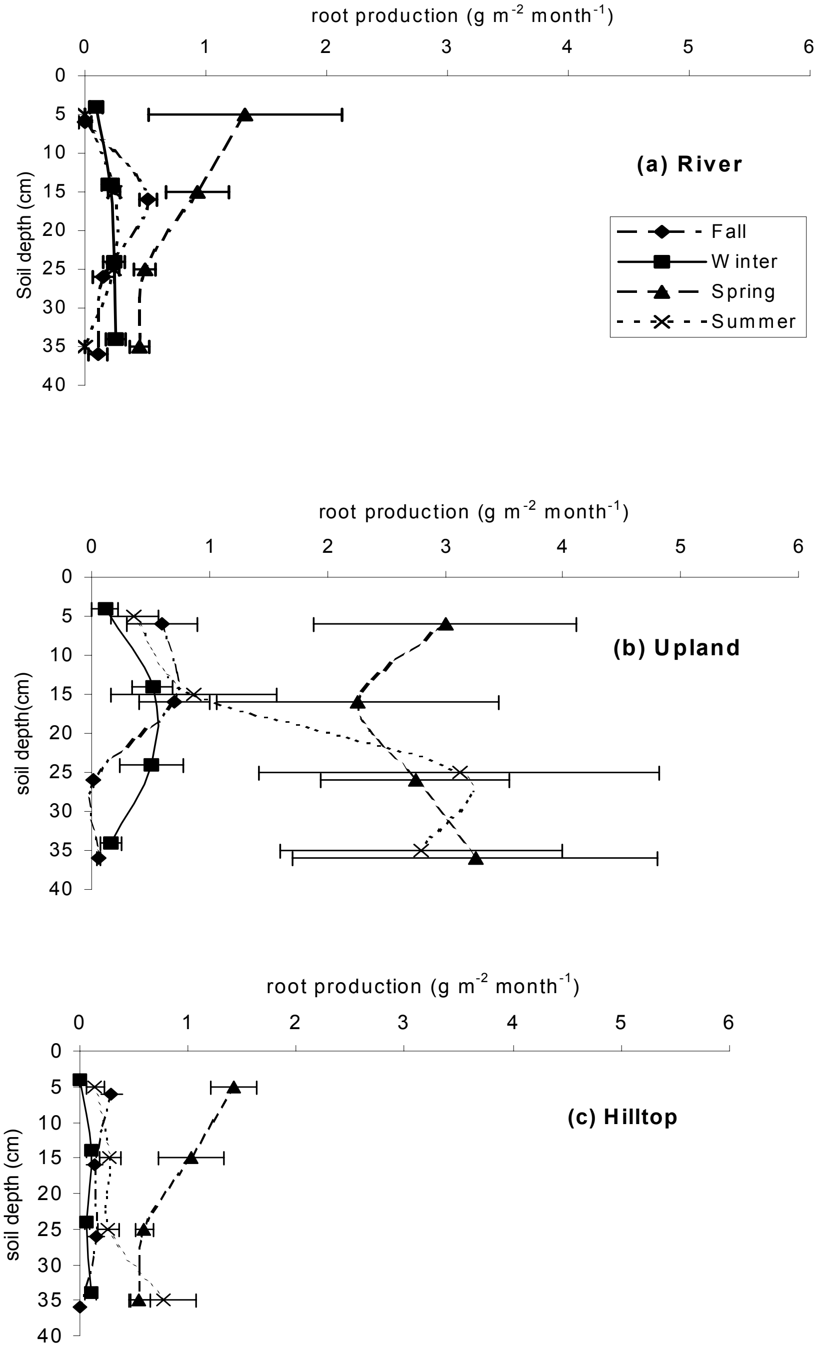

Figure 2—Effects of soil depth on oak fine root production at three blue oak woodland sites: a) River, b) Upland, c) Hilltop. For each season and soil depth, values are means of four to six cores. Bars are standard errors of means. Data from the Upland sites were modified from Cheng and Bledsoe [In press].

Table 1—*Ectomycorrhizal colonization (short-term and long-term studies) at three blue oak woodland sites. In the short-term study, cores were harvested 4 times: winter (Jan 199 –Mar 1998); spring (Apr 1999–Jun 1998); summer (Jul 1999–Sep 1998); fall (Oct 1998–Dec 1998). In the long-term study, cores were harvested after 6 months (Jan – Jun 1998); 9 months (Jan – Sep 1998) and 12 months (Jan – Dec 1998).*

		Sites			
Study	**Interval**	**River**	**Upland**	**Hilltop**	**Mean**
		ectomycorrhizal tips/m root length			
Short-term	Winter	0	0	0	0
	Spring	26	15	0	14
	Summer	0	0	0	0
	Fall	32	19	0	17
Long-term	6 months	75	53	0	43
	9 months	21	9	0	10
	12 months	42	24	0	22

Discussion

Oak fine root production occurred year around *(fig. 1)*, but more than half of the production occurred in spring (58 percent of total). About 28 percent of the production occurred in summer and only 15 percent occurred in fall and winter. We suggest three possible reasons to explain these seasonal patterns. First, soil temperature and moisture are critical factors affecting root growth. Spring is a favorable season for root growth in term of soil temperature and moisture, so it is not surprising that oak fine root production was greater in spring than in other seasons. In summer when soils are very dry, oaks exhibit hydraulic lift and can use subsoil water to extend the growing season of oak fine roots (Huang 1997, Ishikawa and Bledsoe 2000). In our study, we found significant oak fine root production in summer. Similarly, López and others (1998, 2001) also reported that new fine root production of holm oak occurred in summer in Spain. Second, oak fine root production was affected by grass root growth due to competition for soil resources, such as water (Gordon and others 1989) and nitrogen (Welker and others 1991). Increased grass root production may decrease oak fine root production. In fall, after the first rains, grass seeds germinated and grew rapidly. In spring, annual grass flowered and set seed, but grass roots grew very little. In summer, when soils were very dry, annual grasses were dead. Cheng and Bledsoe [In press] reported that grass root production was the greatest in fall and winter; in contrast, oak fine root production was the greatest in spring and summer. Third, timing of root production may be affected by aboveground events (Burke and Raynal 1994, Fahey and Hughes 1994, Hendrick and Pregitzer 1996). In summer, high demand for water and nutrients by the expanding oak canopy stimulated oak fine root growth; while during winter dormancy, oak fine root production was low.

Unlike grass roots, oak fine root production did not show significant differences with soil depth (Cheng and Bledsoe [In press]). In summer, oak fine root production was greater in lower soil depth at both Upland and Hilltop sites, which suggest that oak trees use subsoil water to extend root growth in the dry summer period. Oak fine root production was higher at the Upland site than at the River and Hilltop sites. In contrast, grass root production was higher at the River and Hilltop site than at the Upland site (Cheng and Bledsoe [In press]). There may be both spatial and temporal factors, which differentially affect oak and grass roots production, allowing oak and grass roots to dominate in different seasons and at different sites. Why was oak fine root production so different at the three sites?

Although there were some differences in soil chemical characteristics among three sites *(table 2)*, these soil chemical differences were small and not sufficient to explain why oak and grass root growth patterns were so different among the sites. At the Hilltop site, oak trees were large and widely distributed *(table 2)*, and grass fine root production was high (Cheng and Bledsoe [In press]), reducing oak fine root production by competition for water and nutrients. This may explain why oak fine root production was low at this site. We also hypothesize that smaller oak trees are more active and produce more fine roots. Millikin and others (1997) demonstrated there was linear relationship between the log of DBH and the log of oak large woody root biomass. However there was no information about the relationship between oak DBH and root fine root biomass. At the Upland site, where oak fine root production was highest, some oak trees have double-trunks. Perhaps growth of these trees was vigorous and caused the high production of oak fine roots. Future work is needed to explore why oak root production can vary among sites in the same ecosystem.

Table 2—*Differences in soil (B horizon, 5-40cm) chemical and site characteristics among three blue oak woodland sites. For each soil chemical characteristic, values with same letter were not significantly different ($p > 0.05$). Data were modified from Cheng and Bledsoe [In press].*[1]

Characteristics		River	Upland	Hilltop
Soil	CEC (umol g^{-1})	308.0ab	346.0a	281.0b
	X^a-K (umol g^{-1})	8.8a	3.3c	6.0b
	X^a-Mg (umol g^{-1})	14.8c	72.8a	31.3b
	Avail-P (ug g^{-1})	34.2a	8.4b	15.7b
Site	Elevation (m)	137.0	183.0	404.0
	Stems (per ha)	216.0	205.3	108.9
	Average DBH (m)	0.3	0.3	0.5
	Canopy area (m^2 m^{-2})	0.6	0.4	0.3

[1] X^a = exchangeable.

In the short-term study, ECM infection occurred in different seasons *(table 1)*. In winter and summer, the colonization rate was zero, suggesting that environmental factors played important roles in ECM formation. Soil may have been too dry in summer, too cold and moist in winter for ECM fungi activity. In the long-term study, ECM colonization was highest in the 6-month interval (winter + spring), then decreased after the 9-month interval (winter + spring + summer), and then increased after the 12-month interval (harvested in fall). Both short-term and long-term data showed similar seasonal ECM colonization patterns *(table 1)*. Spring and fall were better seasons for ECM formation than winter and summer. ECM colonization was significantly higher in the 6-month interval of long-term study than in the spring season of short-term study, which suggested that less disturbance (long-term study) increased both oak fine root production and ECM colonization rate. Compared with data from the 6-month interval, the colonization rate in the 9-month interval was 70-80 percent less, probably due to decomposition of roots. Thus, in this California oak woodland, the estimated ECM root lifespan was less than 6 months. Longevity of mycorrhizal roots depends on several environmental factors, such as soil temperature, moisture, nutrient availability, as well as root branching order (Majdi and others 2001). In our study, dry and hot summers adversely affected ECM root longevity, which was much lower than that reported by other researchers (Majdi and others 2001, Majdi and Nylund 1996). The survival and vitality of ECM roots over the summer may enhance water and nutrient efficiency of blue oaks. After one year, ECM colonization rate increased due to formation of new ECM roots in the fall. Surprisingly, no ECM roots were found at the Hilltop site, where grass root production was the highest among three sites (Cheng and Bledsoe [In press]). We assume that soil resources were depleted by grass roots, reducing ECM to zero.

El Niño effects were apparent in 1998, a relatively wet year. Total precipitation in 1998 was 124 cm, which was 40 percent higher than the average level in the adjacent 5 years. In spring the precipitation was 23 cm, much greater than that in 1997 (5 cm) or 1999 (5 cm). Thus, soil moisture may have been higher in 1998 than in other years, perhaps explaining the significant oak fine root growth in the summer of 1998. Long-term observations are needed to study root dynamics in oak woodlands.

Summary

This study reported that oak fine root production was higher in spring with lower, but significant summer growth. ECM colonization occurred mostly in spring and fall. In the long-term study, less disturbance associated with installing ingrowth cores in the long-term study significantly increased ECM colonization. Oak fine root production and ECM colonization were different among three sites, perhaps due to the interacting effects of grass root production and site characteristics. Future work is needed to study root dynamics in different sites and to study competition between blue oak and annual grass roots.

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Turbidity and Total Suspended Solid Concentration Dynamics in Streamflow from California Oak Woodland Watersheds[1]

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Abstract

Resource agencies, private landowners, and citizen monitoring programs utilize turbidity (water clarity) measurements as a water quality indicator for total suspended solids (TSS – mass of solids per unit volume) and other constituents in streams and rivers. The dynamics and relationships between turbidity and TSS are functions of watershed-specific factors and temporal trends within storms and across seasons. This paper describes these relationships using four years of water quality and stream discharge data from seven experimental watersheds in the northern Sierra foothills and north coast oak woodlands of California. Rating curves predicting TSS concentration as a function of turbidity were developed with simple linear regressions. Stream discharge rapidly rose and fell in response to winter storms once watershed soils were saturated. Turbidity and TSS concentrations paralleled this seasonal rise and fall in stream discharge. In addition, a hysteresis effect was observed for both TSS and turbidity during individual storms. Regression slopes for TSS versus turbidity were significantly different between watersheds of similar and differing soils, geology, and hydrology. These results indicate the need for intensive, storm-based sampling to adequately characterize TSS and turbidity in oak woodland watersheds. Water quality monitoring programs that account for the watershed specific nature of turbidity and TSS relationships and the influence that climate, soils, geology, and hydrology have on these relationships will better represent water quality and sediment transport in California oak woodland watersheds.

Introduction

California's oak woodland watersheds provide important ecologic and hydrologic functions. In many cases these watersheds are headwater tributaries for larger river basins and as a result, the quality of water being released from these catchments impacts those watershed functions. For example, increased suspended sediment and turbidity can directly impact aquatic organisms (Sigler and others

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[1] An abbreviated version of this paper was presented at the Fifth Symposium on Oak Woodlands: Oaks in California's Changing Landscape, October 22-25, 2001, San Diego, California.

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1984), alter stream grade, contribute to flooding, and transport a large nutrient flux. Resource agencies and community based resource management programs are developing and implementing watershed management plans to reduce sediment inputs and improve water quality in response to these impacts (CRWQCB 1998).

While site-based erosion inventory and assessments (Lewis and others 2001) are effective means of identifying and mitigating specific sediment sources, in-stream sediment concentration and yield monitoring are important in determining the overall effectiveness of these watershed management efforts. Turbidity has been identified as an effective and inexpensive indicator of suspended sediment (Lewis 1996, Walling 1977). Strong relationships between TSS and turbidity have been repeatedly and consistently identified (Gippel 1995). Turbidity is less expensive and more easily measured than TSS. This provides for the high sampling frequency needed to account for temporal variability in TSS concentrations (Tate and others 1999). For these reasons, turbidity is being promoted as a key parameter for monitoring activities by resource agencies and community-based watershed groups. In order for turbidity to serve as a surrogate for TSS, a numerically defined relationship for predicting TSS as a function of turbidity must be developed from data sets with paired measurements of the two parameters. The objective of our study was to utilize data from seven experimental oak woodland watersheds to: 1) document temporal dynamics of TSS and turbidity; 2) develop relationships for turbidity and TSS for each watershed; and 3) compare TSS and turbidity relationships of each watershed to determine if this changes from watershed to watershed.

Methods

Site Description

The University of California Rangeland Watershed Program began a long-term, watershed scale examination of range management effects on plant community dynamics, hydrology, nutrient cycling, and water quality in 1997. This work was conducted in a network of experimental watersheds at the University of California's Hopland Research and Extension Center (HREC) and Sierra Foothill Research and Extension Center (SFREC) *(fig. 1)*.

The Sierra Foothill Research and Extension Center is located 19 miles east of Marysville, California in the northern Sierra foothills of Yuba County *(fig. 1)*. Elevation ranges from 220 to 2,020 feet (67 to 616 m) and mean annual precipitation is 28 inches (71.1 cm) and ranged from 29 to 52 inches (73.7 to 132.1 cm) during the period of this study (SFREC precipitation records). Water quality and stream discharge monitoring were initiated on three instrumented watersheds (1, 2, and 3) in 1997. Watersheds 1, 2, and 3 are 35, 80, and 116 acres (14.2, 32.4, and 47.0 ha), respectively, and have been managed solely for light to moderate beef cattle grazing since 1965. Watershed soils are formed on basic metavolcanic (greenstone) bedrock (Beiersdorfer 1979) and are Fe-oxide rich, making them resistant to erosion. Soils are classified as Ruptic-lithic Xerochrepts on steep side slopes and Mollic Haploxeralfs on more level areas (Lytle 1998). Vegetation is dominated by blue oaks (*Quercus douglasii*) and intermixed with interior live oaks (*Q. wislizeni*) and foothill pine (*Pinus sabiniana*), typical of Sierra foothill oak woodlands (Griffin 1977). The uneven distribution of trees creates a mosaic of open grasslands, savanna, and woodlands (Epifanio 1989, Jansen 1987).

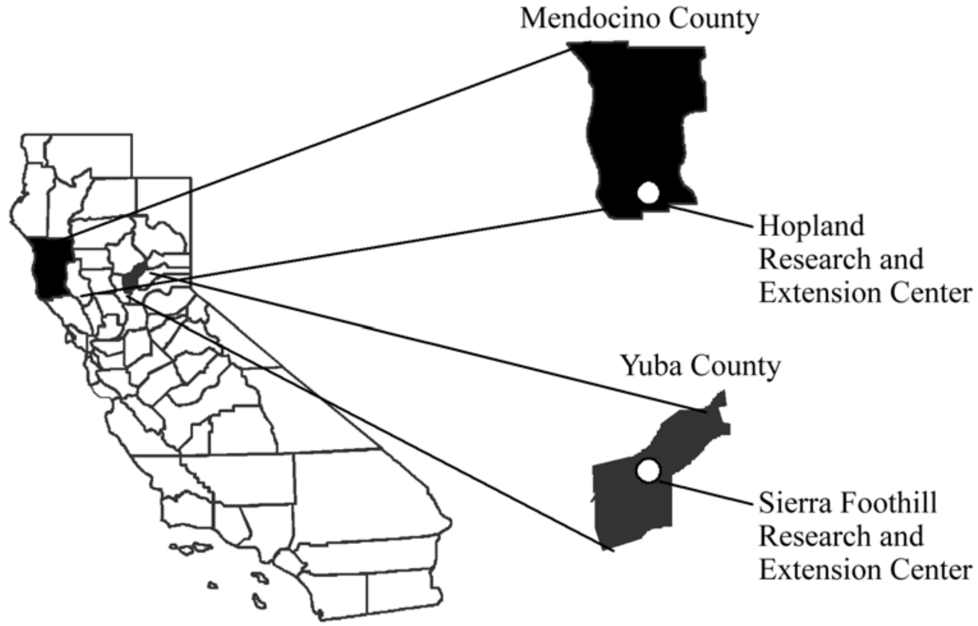

Figure 1—Location of experimental watersheds at Hopland and Sierra Foothill Research and Extension Centers.

The Hopland Research and Extension Center is located 5 miles east of Hopland, California in Mendocino County *(fig. 1)*. Elevation ranges from 440 to 2,670 feet (134 to 814 m) with mean annual precipitation ranging from 37 to 45 inches (94.0 to 114.3 cm) as a function of elevation. During the period of this study, precipitation in the experimental watersheds ranged from 32 to 55 inches (81.3 to 139.7 cm) (HREC precipitation records). Geologically, the area is part of the Franciscan Formation, a mélange of fractured and jointed sandstone and shale (Burgy and Papazafiriou 1974, Gowans 1958). Soils are classified as Typic Agrixerolls and Typic Haploxeralfs (Howard and Bowman 1991). These erosive sedimentary materials and soils are typical of the coastal mountain range. Four experimental watersheds (A, B, C, and D) were established at HREC in 1998. Watersheds A and B are 29 and 22 acres (11.7 and 8.9 ha), respectively, and managed for light to moderate sheep grazing from January to March. Watersheds C and D are 56 and 20 acres (22.7 and 8.1 ha), respectively, and have been excluded from livestock grazing since 1951. The coastal oak-woodland vegetation in these watersheds is a mosaic of open grassland and oak trees comprised of valley oak (*Q. lobata*), black oak (*Q. kelloggii*), coastal live oak (*Q. agrifolia*), blue oak (*Q. douglasii*), and madrone (*Arbutus menziesii*) (Pitt 1975).

Data Collection and Analysis

Stream flow was monitored at flumes installed at the outlet of each watershed. Stage height was measured and recorded on 15-minute intervals using an electronic stage sensor. Stream water samples were collected every 1 to 2 hours during storm events using automatic pump samplers, and every 2 to 3 days during baseflow using grab samples. Data presented in this paper span three water years for HREC (1998-

2001) and four water years for SFREC (1997-2001). A water year begins on October 1 of one year and ends on September 30 of the following year.

For this study, water samples were analyzed for total suspended solids (TSS) and turbidity. Total suspended solids is a parameter used to measure water quality as a concentration (weight of solids/volume of water; mg/L) of mineral and organic sediment. We determined TSS by measuring the weight of dry solid material remaining after vacuum filtration of a known sample volume (50 to 100 mL). Samples were filtered through a 0.45-micron filter in accordance with American Public Health Association protocols (Clesceri and others 1998).

Turbidity is the measurement of water clarity measured as the amount of light that is scattered and absorbed as it passes through a water sample. It is measured with nephelometry methodology and recorded in nephelometric turbidity units (ntu) (MacDonald and others 1991). The amount of light scattered or absorbed changes as a function of the size, shape, surface characteristics, and quantity of particles within the sample (Clifford and others 1995, Gippel 1995). We analyzed samples according to American Public Health Association protocols (Clesceri and others 1998).

Rating curves for TSS as a function of turbidity were developed using linear regression methods with TSS as the dependent variable and turbidity as the independent variable. This analysis does not account for the recognized non-normal distribution of water quality data and the potential need to transform these data. However, watershed groups and other potential generators and users of such data often use simple linear regression; thus, this approach is relevant to their implementation and interpretation of TSS and turbidity relationships.

Curves for each individual watershed, as well as curves for the pooled data from each study site, were developed. The correlation coefficient for these curves indicates the variability between turbidity and TSS across a range of values. Higher correlation coefficients are indicative of lower variability and better prediction of TSS by turbidity. In addition, these curves describe the rate that TSS changes with changes in turbidity through the slope of the regression line. If watersheds have similar TSS and turbidity relationships their rating curve slopes will be similar or homogeneous. Tests of regression line slope homogeneity were made with an F-test (Snedecor and Cochran, 1989) to determine differences of intra- (within sites) and inter- (across sites) watershed TSS and turbidity dynamics. All statistical analyses were conducted utilizing SYSTAT version 9.0 (SPSS Inc., Chicago, IL).

Results

Streamflow in these intermittent streams has three distinct seasonal periods described by Huang (1997) as wetting, saturation, and drying. The 1999-2000 annual hydrographs for Watershed C at HREC and Watershed 2 at SFREC illustrate hydrological and sediment dynamics typical of the watersheds from each site *(figs. 2a,b and 3a,b)*. Discharge was low and constant during the early months of winter. During this priming phase, precipitation infiltrated and recharged watershed soils and did not contribute to noticeable increases in streamflow. Streamflow responses to rainfall became elevated and rapid once soil water storage capacity was approached and the soils were saturated. Results from long-term monitoring indicate that this saturation phase was reached after six to eight inches (15.2 to 20.3 cm) of annual cumulative rainfall have occurred at SFREC (Lewis and others 2000) and eight to ten inches (20.3 to 25.4 cm) at the HREC. Air temperature and evapotranspiration increased and storm frequency and intensity decreased with the onset of spring, resulting in a drying phase in which streamflow gradually declined. Storms during this phase generated increased streamflow, but peak stormflow was less than during the saturation phase.

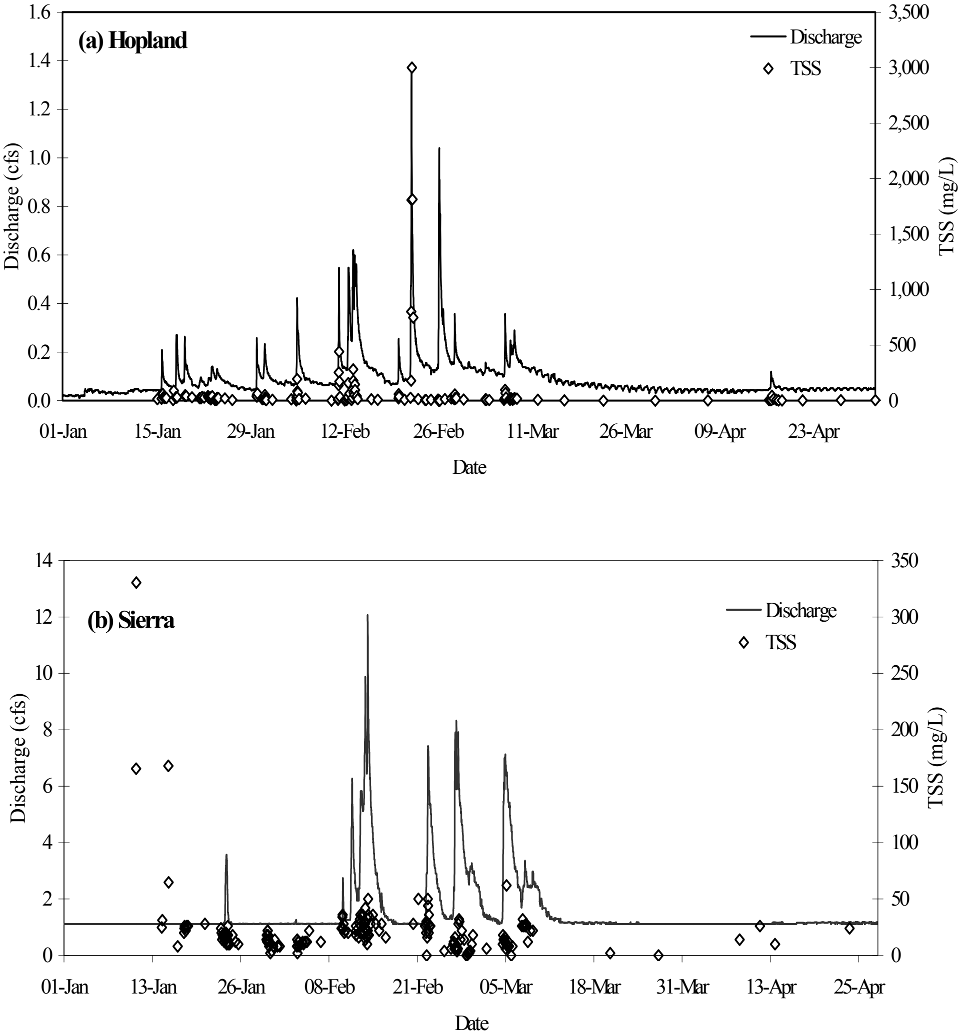

Figure 2—Total suspended solids and stream discharge for 1999-2000 in (a) Hopland Watershed C and (b) Sierra Foothill Watershed 2.

These streamflow phases resulted in seasonal variability in TSS *(figs. 2a,b)* and turbidity *(figs. 3a,b)*. Both TSS and turbidity increased during the transition from wetting to saturation phases. During the drying phase, TSS and turbidity returned to the lower values observed during the wetting phase. Storm variability was also evident for TSS and turbidity *(fig. 4)*. Once in the saturation phase, TSS concentrations and turbidity increased and decreased with the rise and fall of streamflow. Tracking the succession of TSS and turbidity measurements through an individual storm as a function of discharge, it becomes evident that they increased and decreased with similar changes in discharge *(fig. 5)*. Furthermore, higher TSS and turbidity values are observed on the rising limb of the hydrograph as compared to similar discharge values on the falling limb, a phenomenon termed hysteresis.

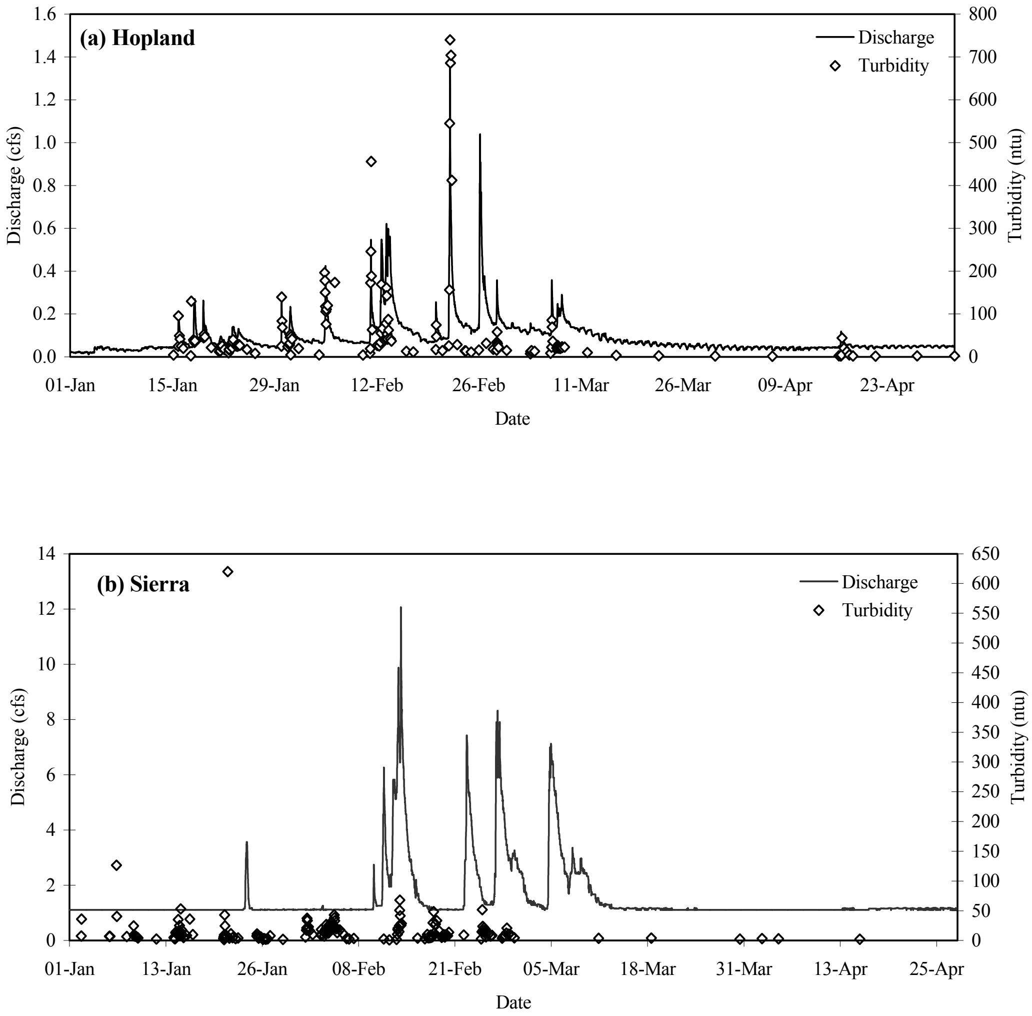

Figure 3—Turbidity and stream discharge for 1999-2000 in (a) HREC Watershed C and (b) Sierra Foothill Watershed 2.

Mean turbidity and TSS concentrations were generally higher for HREC watersheds than for SFREC watersheds *(table 1)*. In addition, variability in both mean TSS and turbidity was higher within the HREC watersheds than in the SFREC watersheds, although, these differences and variability were not always statistically significant. For example, mean TSS concentration from HREC Watershed B was not significantly greater than mean TSS concentration in either SFREC Watersheds 1, 2, or 3. And TSS concentration in SFREC Watershed 3 was not significantly less than values observed in HREC Watersheds A, B, C, or D. The mean TSS and turbidity values for the three SFREC watersheds were not significantly different. By contrast, mean TSS concentration and turbidity in HREC Watershed A were significantly greater than they were in Watersheds B and D.

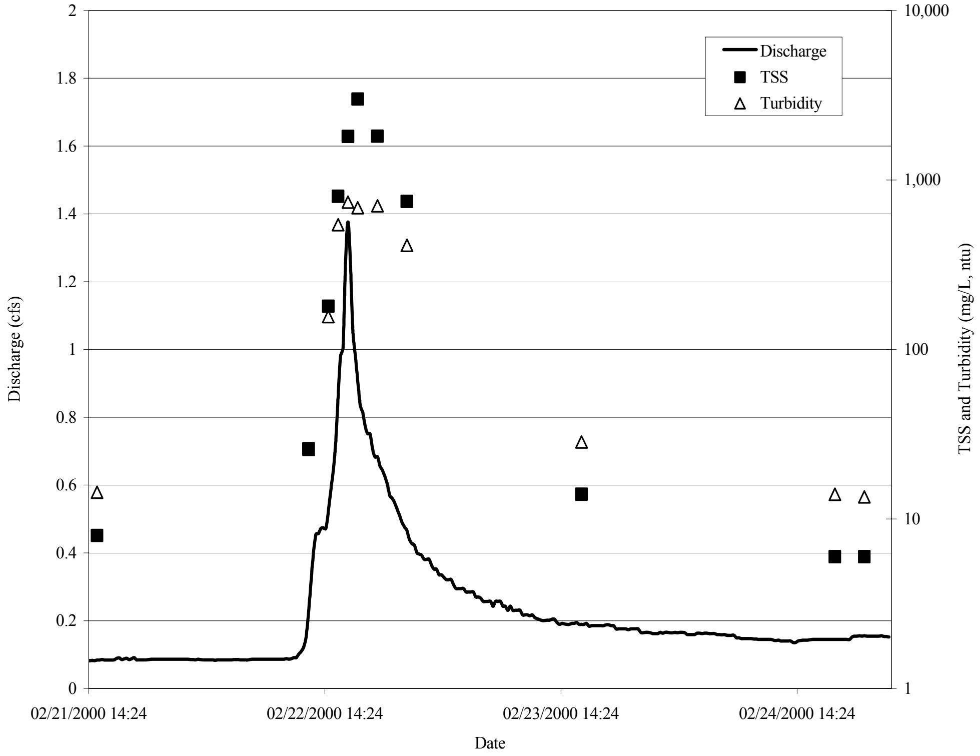

Figure 4—Effect of February 21-24, 2001 storm discharge on total suspended solids (mg/L) and turbidity (ntu) in Hopland Watershed C.

Table 1—*Comparison of total suspended solids (TSS) and turbidity in Hopland (1998-2001) and Sierra Foothill (1997-2001) Research and Extension Center watersheds. Values are means ± standard error of means. Means with different letters are significantly different (p<0.05) within columns.*

Site	Watershed	N	TSS	Turbidity
			mg/L	ntu
Hopland	**A**	396	99.7 ± 9.4a	66.8 ± 5.2a
	B	344	47.6 ± 9.8bc	29.3 ± 3.1bc
	C	366	71.7 ± 11.5ac	61.1 ± 5.9a
	D	268	59.7 ± 5.1c	51.7 ± 4.1a
	Combined	1,374	71.5 ± 4.9d	53.1 ± 2.5d
Sierra	**1**	309	22.2 ± 1.2b	25.3 ± 1.4bc
	2	372	24.5 ± 1.7b	18.2 ± 2.0b
	3	350	46.3 ± 3.3bc	38.5 ± 2.5c
	Combined	1,031	31.2 ± 1.4 e	27.2 ± 1.2e

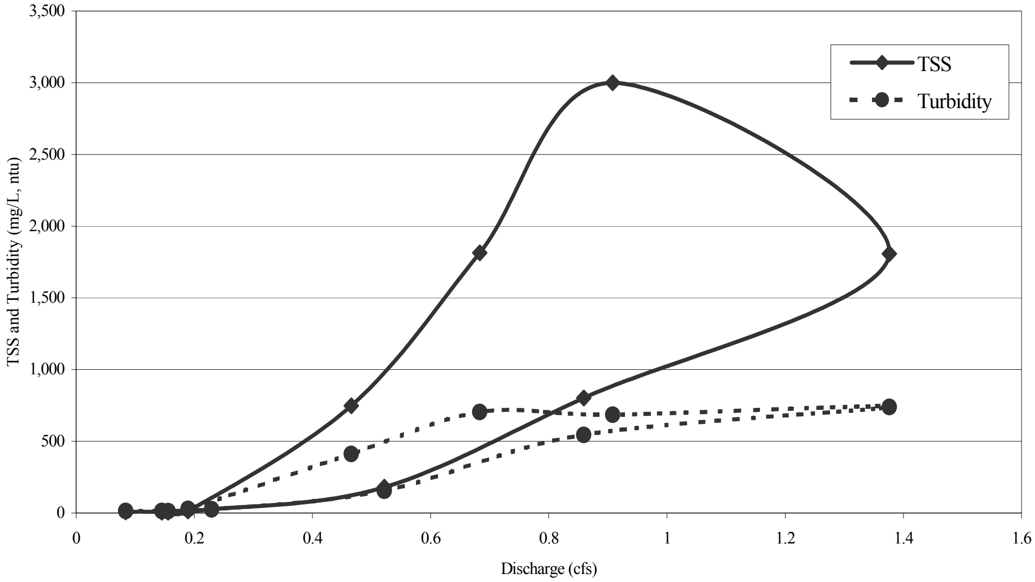

Figure 5—Hysteresis loops for total suspended solids (mg/L) and turbidity (ntu) as a function of discharge (cfs) in Hopland Watershed C from Feb. 21 to Feb. 24, 2001.

Linear regression analysis of TSS concentrations as a function of turbidity identified variability in relationships within and between the HREC and SFREC watersheds *(figs. 6a, b)*. The correlation coefficients for the seven watershed TSS and turbidity regression analyses were all significant (p<0.001). At HREC, with erosive soils derived from sedimentary parent material, turbidity measurements explained from 89 percent (HREC Watershed B) to 58 percent (HREC Watershed C) of the variability in TSS. At SFREC, with relatively more stable soils, turbidity explained 58 percent (SFREC Watershed 1) or less of the variability in TSS. Regression line slopes were significantly steeper at HREC than SFREC. Test for homogeneity of slopes indicates that the seven TSS and turbidity regression slopes are significantly different from each other (p<0.001). Additional iterative tests for homogeneous slopes between the HREC and SFREC watershed regression lines found that all slopes were significantly different from each other *(table 2)*.

Table 2—*Test for homogeneity of regression line slopes within the four Hopland and three Sierra Foothill Research and Extension Center Experimental Watersheds.*

		Hopland				**Sierra**		
Site	**Watershed**	**A**	**B**	**C**	**D**	**1**	**2**	**3**
Hopland	A	1	-	-	-	-	-	-
	B	<0.001	1	-	-	-	-	-
	C	0.003	<0.001	1	-	-	-	-
	D	<0.001	<0.001	0.035	1	-	-	-
Sierra	1	<0.001	<0.001	0.014	<0.001	1	-	-
	2	<0.001	<0.001	<0.001	<0.001	0.016	1	-
	3	<0.001	<0.001	0.008	0.011	<0.001	<0.001	1

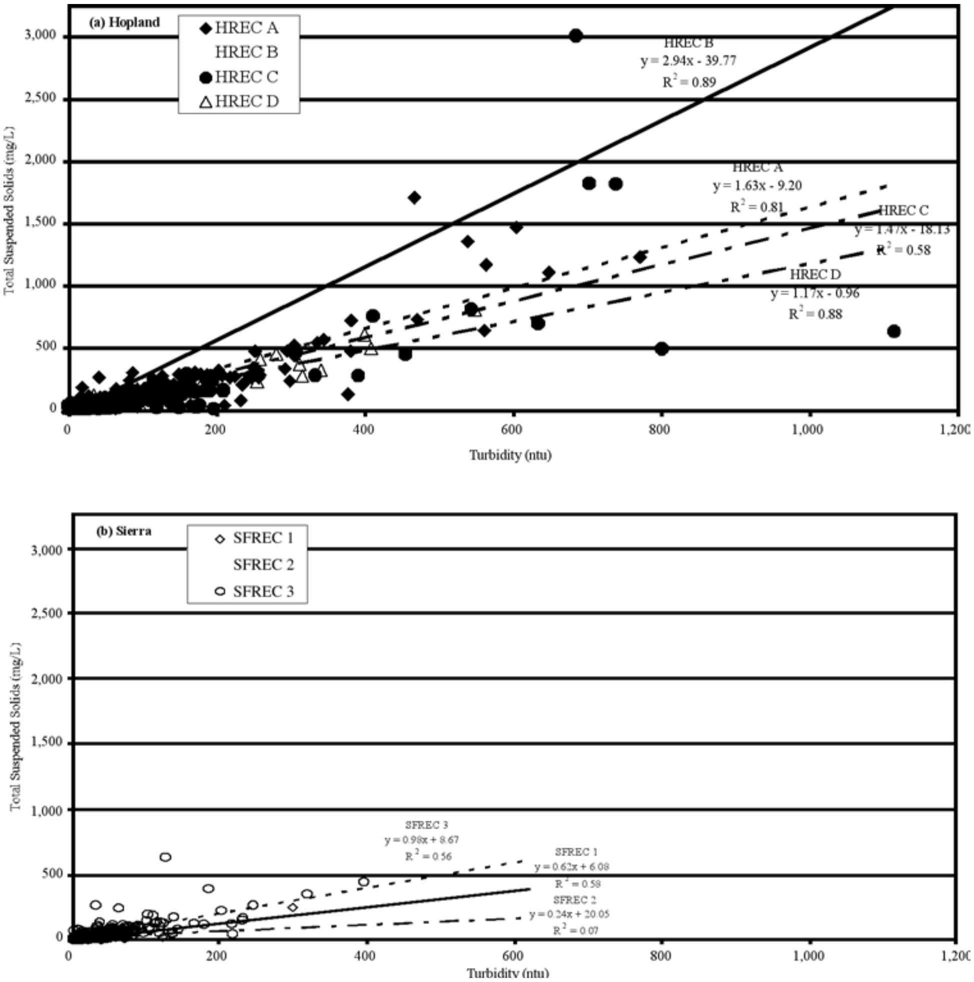

Figure 6—Total suspended solids (mg/L) as a function of turbidity (ntu) in (a) four oak woodland watersheds at Hopland and (b) three oak woodland watersheds at Sierra Foothill.

Discussion and Conclusions

When an indicator of water quality is utilized, such as turbidity, it is important to understand its benefits and its shortfalls. Turbidity is more cost effective than TSS and the relationship between TSS and turbidity is generally strong and well documented. However, it is also site specific. Similar turbidity values from two different tributary watersheds could indicate appreciably different TSS values. This is a result of differences in watershed geology, slope and aspect, soils, vegetation, and land use.

TSS concentrations and turbidity values in California's oak woodland watersheds are variable across seasons and storms and can be explained by the Mediterranean climate and intermittent hydrology of these watersheds. As streamflow rises and falls during storms, TSS concentration and turbidity increase and decrease, respectively. An additional aspect of the storm variability is the demonstrated hysteresis of TSS and turbidity values with regard to discharge, which has been observed in other coastal watersheds (Paustian and Beshchta 1979). The need to account for seasonal and storm variability in water quality monitoring programs has been investigated and discussed previously (Tate and others 1999). Those results combined with this study's results clearly indicate the need for intensive, storm-based sampling for adequate characterization of TSS and turbidity in oak woodland watersheds.

Mean TSS and turbidity within the HREC watersheds were significantly different, and in all but one case, greater than those observed in the SFREC watersheds. Regression slopes greater than one in the HREC watersheds indicated that a greater TSS concentration corresponds to a respective turbidity measurement in HREC watersheds than in SFREC watersheds *(figs. 6a, b)*. On average, HREC receives ten more inches of annual precipitation than SFREC, contributing to differences in rainfall-to-runoff relationships between the two sites and, therein, TSS and turbidity. The soils and geology in the HREC watersheds are considered to be more erosive than those in the SFREC watersheds, contributing to this observed difference. It is also possible that this difference could result from the influence that particle size, sediment composition (organic versus inorganic particles), and water color have on turbidity measurements (Clifford and others 1995, Gippel 1995). Particle-size analysis and comparisons of the organic solid components within HREC and SFREC suspended solids could help in understanding the difference between the two sites.

Comparison of TSS and turbidity regression slopes within each set of experimental watersheds raises questions about the ability to extrapolate between watersheds previously considered to have similar climate, geology, soils, and hydrology. TSS versus turbidity relationships, specifically regression slopes, were significantly different for HREC and SFREC watersheds, *(table 2)*. For example, a monitoring program applying the HREC Watershed D regression relationship of TSS and turbidity to HREC Watershed B would underestimate TSS concentrations by 1, 54, and 60 percent for turbidity measurements of 1, 100, and 1,000 ntu, respectively. In a case where the regression line for SFREC Watershed 3 was applied to Watershed 2, TSS concentrations would be overestimated by 52, 142, and 280 percent for turbidity measurements of 1, 100, and 1,000 ntu, respectively. As indicated in this comparison, error in TSS estimation will depend on the turbidity value because regression slopes are diverging as turbidity increases. The greatest error will occur during storms when the highest TSS concentrations and turbidity values are generated.

This has implications for intended efforts to monitor impacts and benefits from land-use management and watershed restoration on in-stream conditions, as well as environmental regulation based on TSS estimations from turbidity. Turbidity can be utilized as an effective and accurate indicator of TSS concentrations. Because the relationship of these two parameters is watershed specific, water quality monitoring efforts will need to take the time to establish the relationship for each watershed to be monitored. That relationship should be established with data collected across a full range of streamflows to represent the seasonal and storm variability of TSS and turbidity demonstrated in California oak woodland watersheds.

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Nitrogen Dynamics of Spring-fed Wetland Ecosystems of the Sierra Nevada Foothills Oak Woodland[1]

Randall D. Jackson[2] and Barbara Allen-Diaz[2]

Abstract

Spring-fed wetlands are small, highly productive, patchy ecosystems nested within the oak woodland/annual grassland matrix of the Sierra Nevada foothills. In an effort to place these wetlands in a landscape context, we described seasonal variation (1999-2000 growing season) in nitrogen cycling parameters at 6 spring-fed wetland sites of the Sierra Nevada foothill oak woodlands. Ammonium and nitrate pool sizes covaried inversely with nitrate dominance (about 3 μg N g dry soil^{-1}) in autumn/winter during plant dormancy and ammonium dominance (about 6 μg N gds^{-1}) in spring/summer when wetland plants were beginning yearly production cycles. Nitrate is highly mobile in the vadose zone, but can accumulate in the absence of plant growth during dry summer months in the annual grasslands surrounding these wetland systems. With the onset of autumn rains, much of this nitrate may be flushed down slope to spring systems. Spring-fed wetlands may act as either as sources, sinks, or as transformers of this exogenously derived nitrogen.

Introduction

Ecosystem losses of nitrate are of great ecological and economic concern. Eutrophication of aquatic ecosystems can lead to algal blooms and oxygen depletion (Schlesinger 1997). Nitrate pulses in the Mokelumne River watershed have induced downstream eutrophication leading to fish kills in lower river reaches (Holloway and others 1998). From a human health perspective, excessive nitrate concentrations in drinking water (>20 ppm nitrate-N) can cause methemoglobinemia (Bluebaby syndrome, Fan and others 1987, Fan and Steinberg 1996), an ailment which is potentially fatal to infants. The current water standard for allowable nitrate is based on protection from methemoglobinemia. In 1962, the U.S. Public Health Service recommended a maximum permissible level of 10-ppm nitrate-N in drinking water (McKee and Wolf 1963). However, no case of methemoglobinemia has been identified as related to concentrations below about 100 ppm nitrate-N (Fan and Steinberg 1996); 10 ppm nitrate-N is a conservative maximum permissible level. While conservative, this level is deemed appropriate because drinking water is only one of many potential sources of nitrate ingestion. Nitrate spikes (1 to 100 ppm nitrate-N) have been consistently detected during early season storm events in watershed-wide effluent in California hardwood rangelands (Huang 1997, Holloway

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[1] An abbreviated version of this paper was presented at the Fifth Symposium on Oak Woodlands: Oaks in California's Changing Landscape, October 22-25, 2001, San Diego, California.

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and others 1998, Lewis 1999, Tate and others 1999), indicating the potential for these watersheds to act as a net nitrate source to downstream ecosystems.

During summer on California's annual grasslands, the absence of plant uptake, coupled with waning microbial-nitrogen demand, results in mineral nitrogen accumulation (mostly as nitrate) in surface soil horizons (Jackson and others 1988, Dahlgren and Singer 1994, Firestone 1995). With the advent of autumn rains, nitrate becomes highly mobile in the vadose zone (Schimel and others 1989); microbes and germinating annual plants may take up some of this nitrate, but much may be lost via leaching to depths below the rooting zone of annual plants (about 30 cm). Davidson and others (1990) showed that, indeed, some nitrate immobilization occurred with initial autumn rains, however, only at microsites where ammonium was in short supply, as ammonium is the preferred form of mineral nitrogen by most organisms.

Spring-fed wetlands in Californian oak woodlands are first-order riparian areas which are usually situated at slope breaks where steeper slopes give way to more gradual terrain. Nutrient cycling within spring-fed wetlands should be quite different from the surrounding annual grasslands given frequent soil saturation, high primary productivity, and species composition and phenological differences. Furthermore, the typical location of springs (at slope breaks) leaves them ideally situated to act as nutrient traps. We sought to 1) describe intra-annual variability in spring-fed wetland N dynamics, 2) explore the potential for nitrate inputs to spring-fed wetlands from the surrounding annual grassland/oak woodland matrix, and 3) measure spring-fed wetland nitrate outputs.

Methods

Study Area

Owned and managed by the University of California for more than 30 years, the Sierra Foothill Research and Extension Center (SFREC) is located on the western slope of the Sierra Nevada foothills in Yuba County, CA *(fig. 1)*. SFREC covers 2300 ha of steep to rolling landscape, 90-600 m above sea level. Annual precipitation at SFREC averages 72 $cm \cdot yr^{-1}$ with maximum and minimum air temperatures in the region ranging from 32.0°C in July to 2.2°C in January. Soils in this area are generally shallow and classified as Auburn (loamy, Oxidic, Thermic, Ruptic-Lithic Xerochrepts) and Argonaut (fine, mixed, Thermic Mollic Haploxeralfs) series (Herbert and Begg 1969).

Figure 2 depicts four arbitrarily chosen spring sites from four distinct watersheds at SFREC—Poleline Ridge (PR), Fireline Ridge (FR), Forbes Valley (FV), and Campbell Roadside (CR). Two of these sites (FV & CR) supported two distinctive plant communities—cattail (FVT & CRT) and graminoid (FVP & CRP) dominant. Separate plots were established for each community type X site combination, resulting in six sampling units or plots.

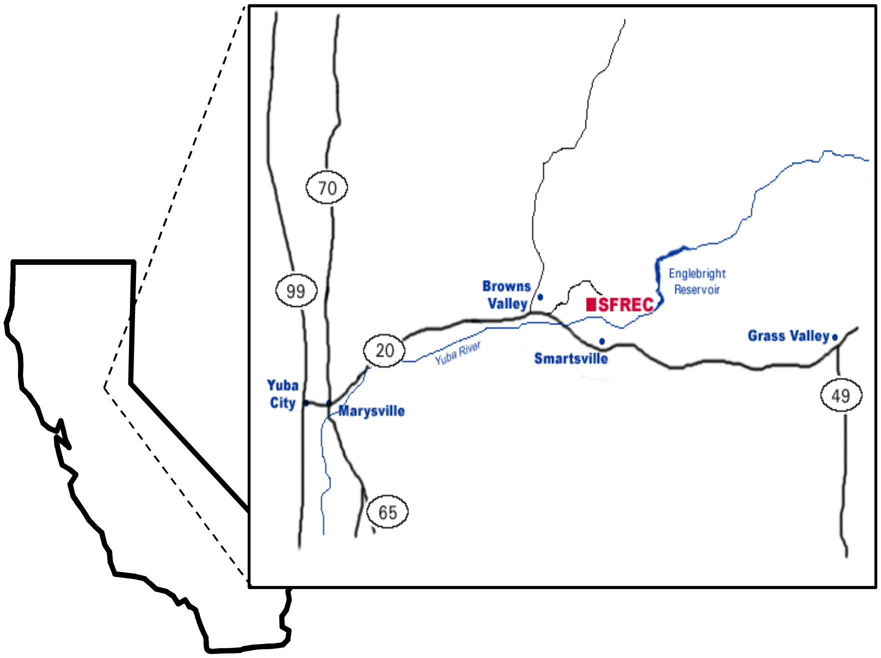

Figure 1—Sierra Foothill Research and Extension Center (SFREC).

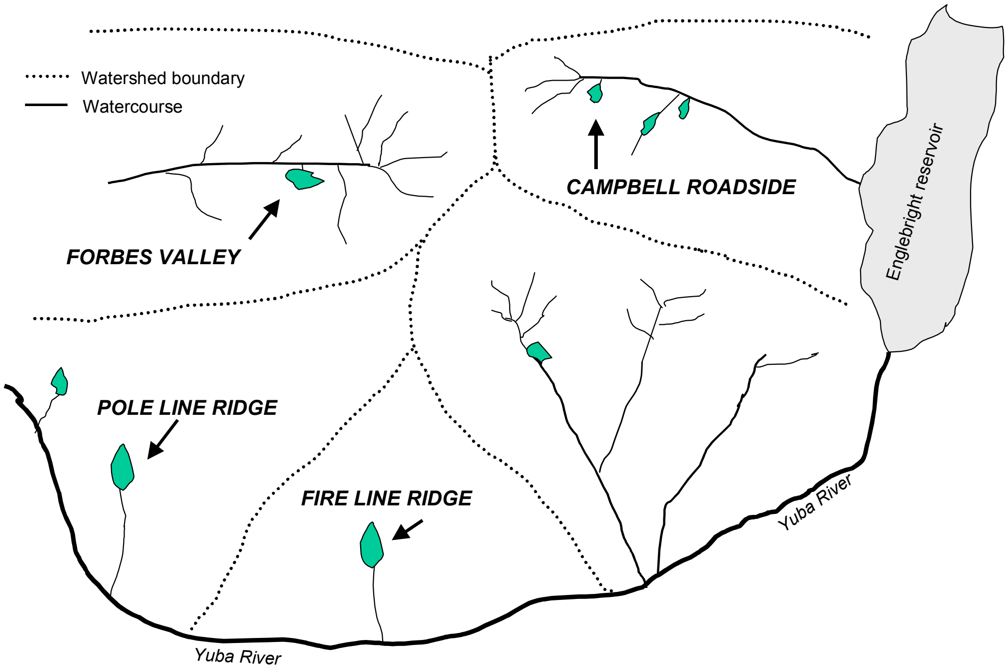

Figure 2—Location of significant spring-fed wetland sites at SFREC.

Wetland Soil N Pools

Wetland soils were collected in September and December 1999 and March and June 2000 from each plot for determination of standing soil N pools. Six soil cores (5-cm diameter X 20-cm deep) were randomly removed from each plot and immediately placed in coolers for transport to the University of California, Berkeley. Cores were stored for a maximum of 48 hours at 4°C prior to hand homogenization to remove roots and rocks. Ten grams of soil were weighed out in duplicate: one subsample for gravimetric water content determination (24 h @ 105°C), and one subsample for immediate extraction in 2*M* KCl. Extracts were frozen prior to ammonium (method #12-107-06-2-A) and nitrate (method #12-107-04-1-B) determination on the Lachat autosampler (Zellweger Analytics).[3]

Soil and Surface Water Sampling

To assess the potential for nitrate losses from annual grassland uplands, we collected leachate from three transects (one directly upslope, two at 45° angles; *fig. 3*) of preinstalled, porous cup leachate samplers (Model 1900, Soilmoisture Equipment Corp., Santa Barbara, CA) radiating up slope from each of two spring sites (PR & FV). Leachate samplers were installed in March 2000 at 5-m intervals along each transect at depths of about 30 and about 90 cm to sample from below the annual grassland rooting zone and just above bedrock *(fig. 3)*. Lateral flow of water and nutrients is mainly confined to these two soil horizons at SFREC, but is differential due to soil textural class separation (Dahlgren and Singer 1994). Hand vacuum pumps were used to apply negative pressure to soil water samplers (about 70 cbars). Soil water samplers were left under pressure until the following sample period (about 4 weeks) so that concentrations from a given date reflected conditions from the previous sampling date. In several trials, the volume of water extracted reached an asymptote after 2 to 6 days, i.e., little more could be withdrawn from the soil matrix. We were not concerned about denitrification of standing samples because the porous cups of these lysimeters are impermeable to organic matter which is requisite as a labile carbon source for denitrifying bacteria (Firestone 1980, Firestone and Davidson 1989).

When available, upland leachate and wetland surface water were collected on a monthly basis throughout the 2000/01 rain season. Within wetlands, about 10 surface- water samples were collected to assess nitrate output from these systems and to compare output with upland soil nitrate dynamics. All water samples were immediately placed in coolers for transport to UC Berkeley whereupon they were frozen until analysis for nitrate at UC Berkeley's Department of Agriculture and Natural Resources laboratory using the method treated by Carlson (1978).

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[3] Mention of trade names or products is for information only and does not imply endorsement by the U.S. Department of Agriculture.

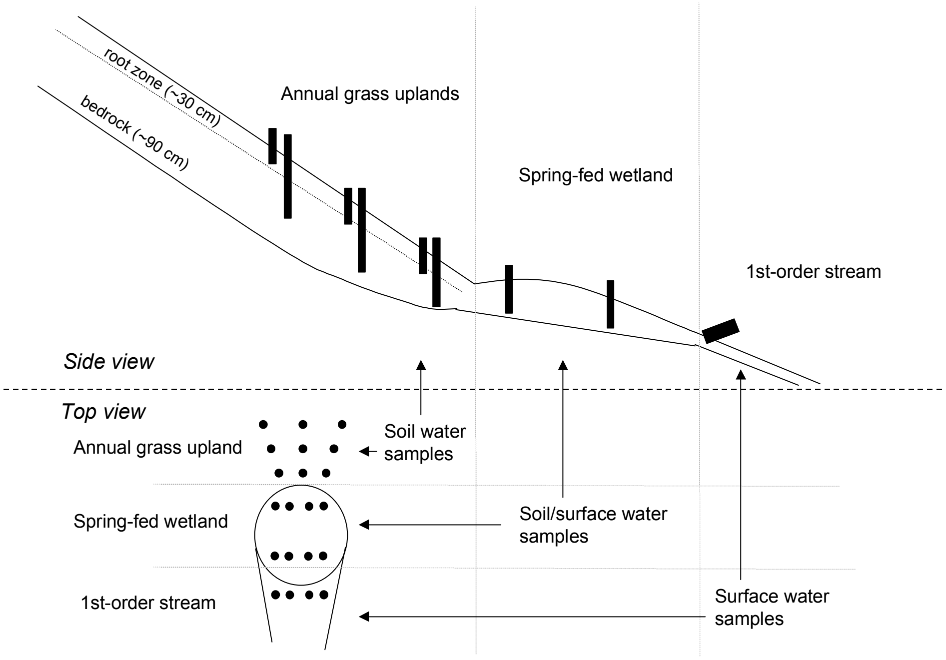

Figure 3—Soil and surface water sampling layout from side and top views.

Results

Wetland Dynamics

Gravimetric water content (GWC) patterns for wetland soils were site specific *(fig. 4)*. Interestingly, the CRT and CRP plots were more similar to the wetter plots (PR and FVT) in autumn and winter, but drier and more similar to the driest plots (FR and FVP) in spring and summer. All but FVT showed an apparent autumn rain response, i.e., $GWC_{December}>GWC_{September}$ for gravimetric water content. Both CRT and CRP displayed steadily declining GWC after brief autumn response, while PR and FVT steadily increase GWC through winter and spring months. Finally, FR and FVP initially responded to autumn rains, but underwent very gradual decline throughout the growing season; overall, these two plots were significantly drier.

During plant dormancy in autumn and winter, nitrate was the dominant form of mineral nitrogen (3.27 µg NO_3^--N g dry soil^{-1} and 2.63 µg NH_4^+-N g dry soil^{-1}, *fig. 5*), whereas ammonium was roughly double nitrate in spring and summer (5.08 µg NO_3^--N g dry soil^{-1} and 6.30 µg NH_4^+-N gds^{-1}), when wetland plants were beginning yearly production cycles.

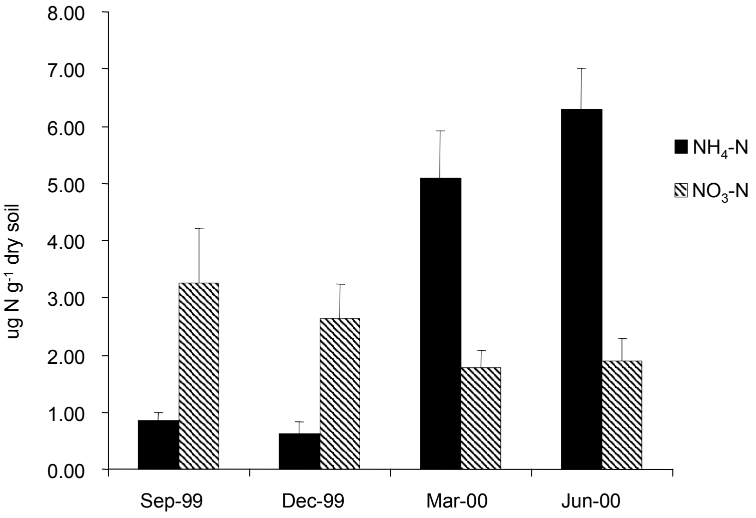

Figure 4—Mineral nitrogen pool sizes averaged over six spring-fed wetland plots.

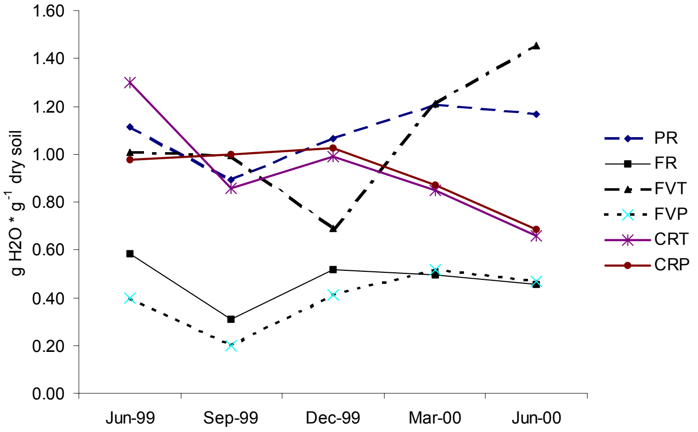

Figure 5—Gravimetric water content of six spring-fed wetland plots.

Upland-wetland Throughput

Surface waters of wetlands showed a general pattern of relatively constant nitrate concentrations through the summer and early autumn (about 0.20 ppm nitrate-N), with marked increase during winter months and a peak for the period representing late January through early February (0.69 ppm nitrate-N, *fig. 6*). However, nitrate patterns in upland leachate were temporally variable. We were unable to recover any upland leachate during summer and early autumn. Leachate was finally realized in mid-November, a sample period reflecting late October conditions, which coincided with a cumulative total of about 30 mm rainfall for that season *(fig. 7)*. During this period, mean nitrate concentrations were exceptionally high (41 ppm nitrate-N) but decreased over the remaining winter months to less than 1 ppm nitrate-N. Nitrate concentrations from 30- and 90-cm were averaged as no significant differences were determined between these depths.

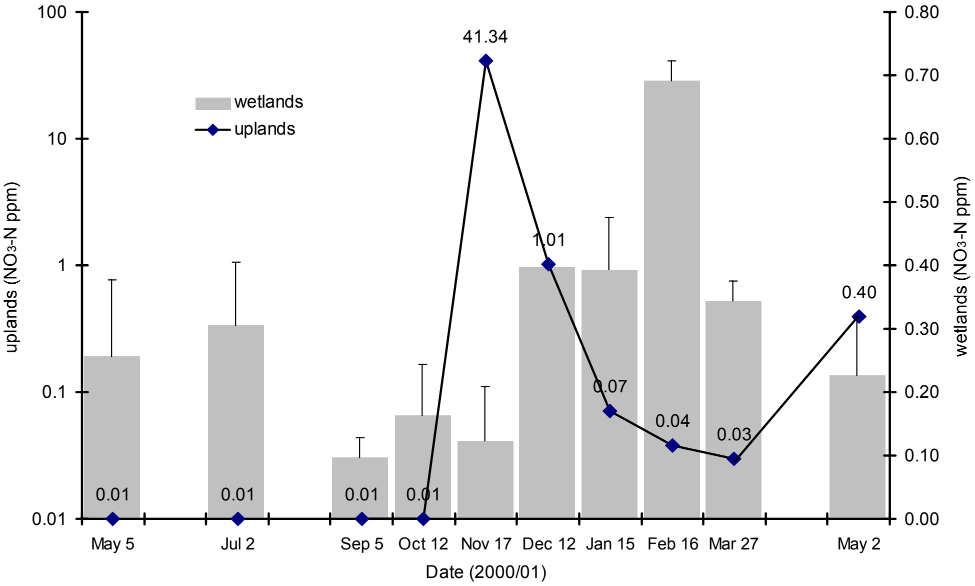

Figure 6—Soil and surface water nitrate concentrations in spring-fed wetlands and surrounding annual grassland upland matrix. Note log scale for primary y-axis.

Discussion

What was the fate of nitrate observed in the annual grasslands above the spring-fed wetlands in the late October/early November period? As rainfall accumulated, effectively priming the dry uplands, a wetting front slowly moved down through the soil profile (Huang 1997). In our study, this front appeared to have transported nitrate that had accumulated during summer in the uplands below the annual grassland rooting zone. Most of this nitrate is generated in the surface soil (0-10 cm) where biological activity is concentrated (Hart and others 1993, Schimel and others 1989). At both 30- and 90-cm soil depths, we observed high nitrate concentrations at the November 17 sampling date. This sample represented nitrate-accumulating conditions that occurred since the previous sampling date (October 12). Prior to October 12, little rain had fallen (about 25 mm), but subsequently, an additional 60 mm of rain fell (October 12-November 17). Apparently this was sufficient to carry nitrate to both sampling depths. The wetting front probably was not linear and macropore flow a likely major pathway for downward transport, resulting in no differences between sampling depths.

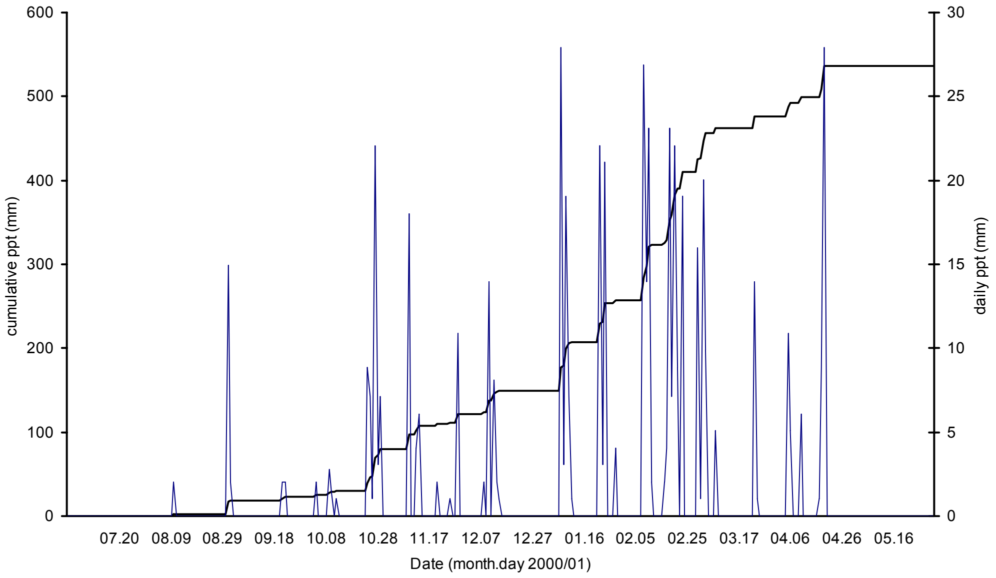

Figure 7—Daily and cumulative rainfall for the 2000/01-water year at SFREC.

By December, it appeared that the front had almost completely flushed the vadose zone of this nitrate pool. A concomitant increase in January and February nitrate concentrations within the surface water of the wetlands indicated that at least some of the upland-derived nitrate probably entered the wetland area. However, we never observed nitrate concentrations >1 ppm, as others have found in higher order streams (Holloway and others 1998, Tate and others 1999). We suggest four possible explanations for this apparent lack of response. First, the pulse of nitrate may have passed through the system undetected. Second, a significant dilution from non-vadose zone ground water may have occurred. Third, the nitrate may have been lost to deep percolation. Lastly, nitrate may have been sequestered by plants, microbes, and/or soil organic matter. These alternatives are discussed in the following sections.

Pulse Not Sampled

Our monthly sampling may have missed spikes of nitrate moving through the system. However, hourly sampling of Tate and others (1999) from SFREC's Lewis watersheds illustrated that major spikes (3-4 ppm) were apparent for weeks, depending on the intensity and duration of storm events. In another SFREC watershed (Schubert), which is known to have at least four spring-fed riparian zones, nitrate concentrations in stream flow were low (0.5-2 ppm nitrate-N), with spikes as high as 60 ppm nitrate-N (Huang 1997, Lewis 1999). These comparisons must be made with caution; variable source areas may contribute to these disparities. As Tate and others (1999) discussed, total nitrogen load (concentration X flow rate per unit time) is the best metric for between-watershed comparisons.

We estimated September flow rates at our first-order spring-fed wetlands (area-velocity method) to range from 0.001-0.02 $L \cdot s^{-1}$, compared to the higher order stream output at SFREC's Schubert and Lewis watersheds of about 0.1-400 $L \cdot s^{-1}$. Given the seasonal variation of nitrate-N concentrations we observed in spring-fed output (0.01-1.5 ppm), and assuming a mean flow rate of 0.007 $L \cdot s^{-1}$, the calculated total N load from these systems ranges from a very conservative estimate (i.e., 0.01 ppm nitrate-N for 12 months) of 0.11 kg $N \cdot y^{-1}$ to an overestimate (i.e., 1.5 ppm nitrate-N for 12 months) of 15.89 kg $N \cdot y^{-1}$. Upland areas above springs in these watersheds average about 2 ha, therefore, we estimate an average watershed load of 0.55-7.95 kg $N \cdot ha^{-1} \cdot y^{-1}$. Total N inputs and outputs to these oak woodland/annual grassland systems has been estimated at about 3 kg $N \cdot ha^{-1} \cdot y^{-1}$ (Dahlgren and Singer 1994). Given the seasonal variability in nitrate concentrations, e.g., about 1 ppm observed in spring output for only about 3 months, this estimate seems quite plausible. Therefore, if pulses of nitrate >1 ppm passed through these spring-fed wetlands with any regularity, nitrogen inputs to the upland watersheds would need to be much higher to maintain overall system nitrogen balance, hence, productivity. This argues for much of the leachate nitrate observed in the annual grassland uplands in autumn being conserved within the watershed in some fashion.

Dilution

Our second alternative explanation for the apparent lack nitrate transfer from uplands to wetlands was that nitrate was diluted by non-vadose zone water, i.e., ground water. This seems unlikely given our observation of very low baseline flow (about 0.001 $L \cdot s^{-1}$) in September prior to initiation of autumn rains. This low volume was likely not sufficient to dilute the nitrate carried in about 50 cm worth of rainfall-derived, vadose flow. In other words, most of the water emanating from springs is vadose-zone derived, so likely not significantly diluted by groundwater.

Deep Percolation

Huang (1997) showed that about 7 percent of the precipitation that fell and was not evapotranspirated in autumn went to deep percolation, while the remaining 93 percent moved laterally through the vadose zone until reaching surface water outlets. This 7 percent equated to about 5 mm of the total 107 mm of rainfall observed during the soil-wetting phase of early autumn. We estimated that the autumn nitrate pulse we observed was carried down through the soil profile in about 50 mm worth of rainfall, since a total of 80 mm was observed by November 12 sampling date, and about 30 percent of this was likely lost to evapotranspiration. With an additional 60 mm of rain between November 12 and December 12, we no longer observed extremely high nitrate concentrations. According to Lewis (1999), about 150 mm rainfall are needed before downward flow gives way to significant lateral flow. Nitrate may have been lost to depth during this period, or it may have remained at the wetting front before being "pushed" through to surface waters when about 150 mm rain had accumulated, i.e., late December.

Wetland Sequestration

Our relatively high nitrate concentrations across all months in wetland soil extracts indicate potential for wetlands to trap inputs. The semi-saturated to saturated soil conditions should preclude nitrification of ammonium because it is an obligately aerobic process (Paul and Clark 1996). Once exogenous nitrate has found the wetland, it should be subject to any combination of plant and microbial uptake, soil organic matter adsorption, dissimilatory nitrate reduction to ammonium (Silver and others 2001), or denitrification [$NO_3^- \text{->} N_2O_{(g)} + N_{2\,(g)}$]. However, apparently very little of this nitrate is throughput to stream waters, or it is effectively baffled such that stream water concentrations remain low, but consistent (sensu Campbell and Allen-Diaz 1997). Regardless of the sequestration mechanism, exogenous nitrate likely plays an important role in maintaining the productivity of these wetland systems. Likewise, the productivity of these systems affords the important ecosystem service of nutrient conservation at the small catchment scale.

Acknowledgments

Caroline Bledsoe and one anonymous reviewer provided thoughtful comments on earlier versions of this manuscript. Thanks to Ken Tate and Theresa Ward for grueling excavation labor and Karen Haubensak, Letty Brown, Bryan Qualls, Michele Hammond, Theo Leung, and Jennie Kluse for sampling help. The Integrated Hardwood Range Management Program supported this work.

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Factors Influencing Soil-Surface Bulk Density on Oak Savanna Rangeland in the Southern Sierra Nevada Foothills[1]

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Abstract

The objectives of this study were to compare soil-surface bulk density between rangeland pastures not grazed since 1935, 1975, and 1995 to grazed areas with a 15-year record of light (>1,000 lbs ac^{-1} RDM), moderate (600-800 lbs ac^{-1} RDM), and heavy (<400 lbs ac^{-1} RDM) grazing by beef cattle; and to determine the influence of oak canopy, topographic position, and livestock concentration activities on bulk density. The study was conducted on sandy-loam soils on oak savanna at the San Joaquin Experimental Range in Madera County, CA. A total of 1047 bulk density samples were collected. Soil-surface bulk density was 19 percent lower under oak canopy than in adjacent open grasslands. Livestock grazing at all levels increased bulk density above that in areas excluded from grazing for 5, 25, and 65 years, while there were no significant differences among exclosures. Areas with light grazing had lower bulk density than moderately and heavily grazed sites, which were not different from each other. RDM recommendations at, or above, 800 lbs ac^{-1} will likely lead to reduced soil-surface bulk density on these soil series. Livestock-concentration areas were the most compacted sites in the study.

Introduction

Oak woodlands cover an estimated 3 million ha in the interior valleys and foothills of central California (Griffin 1977), providing forage, firewood, wildlife habitat, open space, and domestic water supplies. The quality of much of California's surface water is dependent on the condition and management of the soils on these watersheds. Blackburn (1984) summarized the general concerns that livestock production practices lead to soil compaction which reduce soil porosity and infiltration capacity, leading to increased surface runoff, soil erosion, and transport of non-point source pollutants.

The most commonly reported measure of soil compaction is soil dry bulk density, expressed as the oven dry mass of soil per volume of soil (g cm^{-3}) (Blake and Hartage 1986). Several rangeland studies have shown that soil bulk density is negatively correlated with infiltration capacity and positively correlated with surface runoff (Liacos 1962; Packer 1953, 1963; Rauzi and Hanson 1966; Spaeth and others

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1996). Liacos (1962) found that the soil-surface bulk density on ungrazed [residual dry matter (RDM) ~ 3,400 lbs ac^{-1}] Los Osos clay loam soils east of Berkeley averaged 1.4 g cm^{-3}; sites grazed heavily (RDM ~ lbs ac^{-1}) averaged 1.6 g cm^{-3}; and sites that were lightly (RDM ~ 1,250 lbs ac^{-1}) grazed were intermediate. On coarse sandy loam soils at the San Joaquin Experimental Range (SJER) north of Fresno, Ratliff and Westfall (1971) found that soil-surface bulk density was 24 percent lower within a 36-year ungrazed pasture than on grazed sites. Also at SJER, Assaeed (1982) observed higher bulk densities on grazed swale sites (1.38 g cm^{-3}) compared to 10 year ungrazed swale sites (1.22 g cm^{-3}). However, Assaeed (1982) found no difference in bulk density between grazed and ungrazed areas located on hill-slope positions. These studies indicate that grazing in general will increase soil bulk density compared to no grazing, and the authors hint that topographic position may play a role in determining bulk density. The questions of how oak canopy, time since removal of grazing, and grazing intensity affect bulk density are still outstanding, as are the questions of how these factors might interact to determine grazing effects on bulk density. In this paper we present preliminary results of an on-going study to address some of these questions.

The objectives of this study were to compare soil-surface bulk density between rangeland pastures not grazed since 1935, 1975, and 1995 to grazed areas with a 15-year record of light (>1,000 lbs ac^{-1} RDM), moderate (600-800 lbs ac^{-1} RDM), and heavy (<400 lbs ac^{-1} RDM) grazing by beef cattle; and to determine the influence of oak canopy (blue oak, live oak, open), topographic position (swale, hill-slope, ridge), and livestock concentration activity (none, trails, corrals, supplement sites, water tanks) on soil-surface bulk density.

Methods

Study Site

The study was conducted on the 1,772 ha San Joaquin Experimental Range (SJER) in Madera County, CA. SJER has been operated by the USDA Forest Service as a rangeland research station since 1932. SJER is grazed year around with a commercial type beef cattle herd. Elevation ranges from 213 m to 518 m. Climate at SJER is Mediterranean with 485 mm average annual precipitation falling almost entirely during November to May as rainfall. Soil type is uniform across SJER with the Ahwahnee Series (coarse-loamy, mixed, thermic Mollic Haploxeralf) in upland (hill-slope and ridge) positions and the Visalia Series (coarse-loamy, mixed, thermic Pachic Haploxeralf) in swale positions. Soil depth in the uplands ranges from 0.5 to 1.0 m. Soil depth in swales can range from 1.0 to 3.0 m.

Swales on SJER are intermittent wetlands which become saturated during the rainfall season, gradually drying as the rainfall season ends. As a result, swales produce green forage later into the summer months than adjacent uplands, making swales a preferred site for livestock. Vegetation is oak woodland/savanna with annual grassland understory. Blue oak (*Quercus douglasii* Hook and Arn.) and interior live oak (*Quercus wislizeni* A.DC.) dominate the overstory, while wild oats (*Avena fatua* L.), ripgut brome (*Bromus diandrus* Roth), soft chess (*Bromus rubens* L.), and redstem filaree (*Erodium cicutarium* (L.) L'Her) dominate the open grassland and understory.

Over the course of years numerous livestock exclosures have been constructed and maintained on SJER for various research related purposes. The size of these exclosures varies from 160 to 0.5 acres. Livestock exclosures constructed in 1935 (~160 ac), 1975 (~20 ac), and 1995 (~15 ac) were selected for use in this study because they span a significant window of livestock exclosure and provide adequate areas for replicated sampling. Annual fall residual dry matter (RDM) mapping has been conducted across SJER since 1985, providing a total of 15 years of grazing intensity history as measured by RDM. GIS technology was utilized to generate a composite RDM map from these 15 years (*fig. 1*).

Design

This study was a cross-sectional survey of soil-surface (0-7.5 cm) bulk density across all available combinations of four factors across SJER. The four factors were grazing history (excluded 1935, 1975, 1995; light, moderate, heavy grazing), canopy (no canopy, blue oak, live oak), topographic position (swale, hill-slope, ridge), and livestock concentration activities (none, supplement station, stock trail, water tank, corral). Bulk density sampling was conducted within the three livestock exclosures as well as within multiple areas with a clear 15-year record of light (>1,000 lbs ac^{-1} RDM), moderate (600-800 lbs ac^{-1} RDM), and heavy (<400 lbs ac^{-1} RDM) grazing (*fig. 1*). Random sampling of available canopy, topographic position and livestock concentration activities combinations was conducted within each grazing history. Where there was oak canopy, trunk diameter at breast height (DBH) was measured. At this point in time, most, but not all, possible combinations of grazing history, topographic position, and canopy have been sampled within the 1935 exclosure, light, moderate and heavy grazing sites. The 1975 and 1995 exclosures do not contain certain combinations involving canopy and topography. For instance, the 1995 exclosure does not contain a canopy by swale combination, and the exclosures do not contain livestock concentration activity.

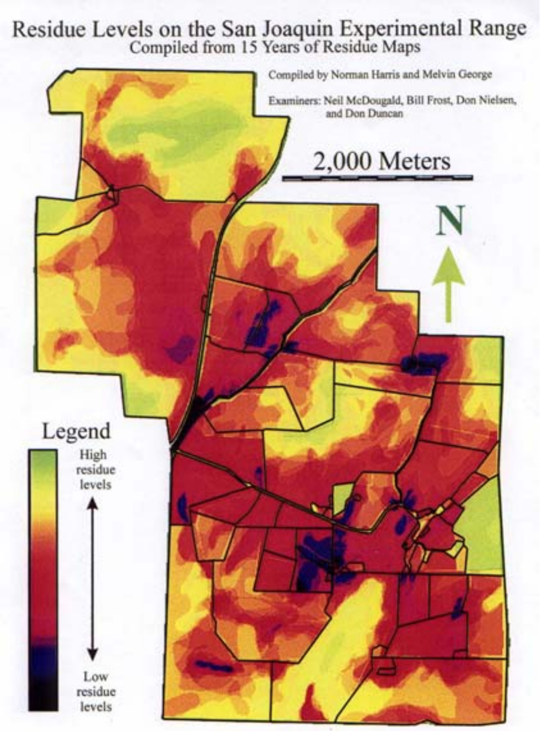

Figure 1—Fifteen-year composite end of season (October) residual dry matter map of SJER.

Soil Dry Bulk Density

Soil-surface bulk density (g cm^{-3}) was determined via the core method (Blake and Hartage 1986) using a 7.62 cm long by 4.78 cm diameter cylindrical metal core. Samples were dried at 105 C for 24 hours in a forced-air oven, weighed and bulk density calculated as sample dry weight (g) divided by sample volume (136.74 cm^{-3}). A total of 1047 bulk density samples were collected across SJER during the fall and early winter of 2000, prior to soil saturation.

Analysis

Data were analyzed via backward stepwise general linear model procedures in Systat V.10 (SPSS, Inc. 1996). Independent variables included in the original model were grazing history (excluded 1935, 1975, 1995; light, moderate, heavy grazing intensity); topographic position (swale, hillslope, ridge); canopy (open, blue oak, live oak); and livestock concentration activity (none, supplement station, stock trail, water tank, corral). Soil-surface bulk density was the dependent variable. Evaluation of interactions between main factors is not reported in this preliminary paper due to insufficient sampling of all possible main effect combinations. On-going sampling will allow this analysis prior to final publication in an appropriate journal. Test criteria for inclusion in the final model was $p<0.05$. Mean separation for significant factors was accomplished using pair-wise contrasts ($p<0.05$). Finally, possible relationships between oak tree size and soil-surface bulk density were evaluated with simple linear regression with soil bulk density as the dependent and DBH as the independent variable.

Results and Discussion

General linear models analysis produced a final statistical model ($p<0.001$, multiple $R^2 = 0.58$, n = 1,047) showing canopy, grazing history, and livestock concentration activity as highly significant factors determining soil-surface bulk density ($p<0.001$). Topographic position was not a significant factor in this model ($p=0.62$). This potentially conflicts with findings by Assaeed (1982) that while swale site bulk density was higher in grazed compared to 10-year exclosures, hillslope bulk density was not significantly different between grazed and ungrazed. Our analysis did allow us to examine the effect of topography with the effect of grazing already accounted for statistically, which we are not certain Assaeed did. It is also possible, in fact likely, that some grazing history by topographic position interactions exist, which our continued data collections will allow us to test.

Canopy

While bulk density was significantly lower ($p<0.001$) under both blue and live oak compared to open areas, there was no significant difference ($p=0.64$) between live or blue oak canopy (*fig. 2*). Oak trees play an important role in determining soil bulk density on oak woodlands. This result is in agreement with work conducted by others illustrating that oaks create islands of enhanced fertility beneath their canopy through organic matter incorporation and nutrient cycling, leading to elevated soil quality relative to adjacent grasslands (Kay 1987, Jackson and others 1990, Dahlgren and others 1997). Low soil-surface bulk density is one component of high soil quality. While the presence or absence of oak canopy was a significant factor determining bulk density, tree DBH (reflecting age) was not a significant predictor of bulk density under either blue (multiple $R^2 = 0.017$) or live (multiple $R^2 < 0.001$) oak canopy.

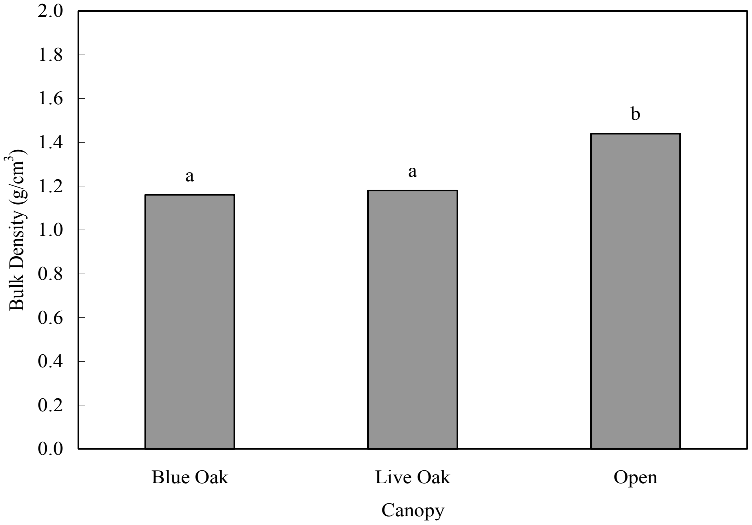

Figure 2—Mean soil-surface bulk density for blue oak, live oak, and open canopy sites at SJER (columns with different letters are significantly different [P $\leq$. 05] by pairwise contrasts).

Grazing History

There was no significant difference in bulk density between the three livestock exclosures; however, all currently grazed sites (light, moderate, heavy) had significantly higher bulk density compared to exclosures (*fig. 3*). Sites with light grazing had significantly lower ($p<0.05$) bulk density than moderate and heavily grazed sites. There was no significant difference between moderate and heavy grazing sites ($p=0.21$). These results compare well with previous work documenting the reduction in bulk density with livestock exclosure (Assaeed 1982, Liacos 1962, Ratliff and Westfall 1971) conducted on California hardwood rangeland. Our results do imply that there is no apparent improvement in soil bulk density past 5 years of livestock exclosure, indicating that the reversal of soil compaction from grazing on these low clay-silt, high sand content, soil types is relatively rapid. One potential mechanism is an increase in activity of burrowing mammals within exclosures, which was our casual observation. Another mechanism could be increased soil organic matter and development of a deeper and more porous 0 horizon within the exclosures. Samples are currently being analyzed for organic matter and organic carbon content.

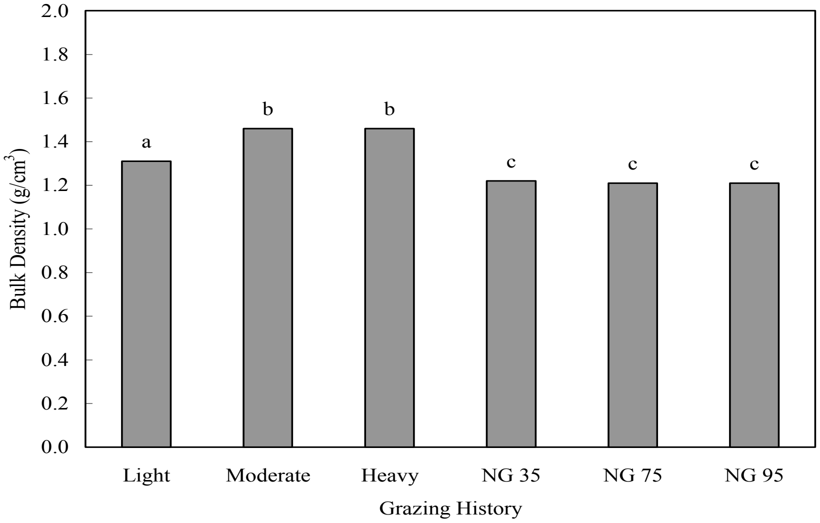

Figure 3—Mean soil-surface bulk density for 15-year light, moderate, heavy grazed as well as pastures excluded from grazing since 1935 (NG35), 1975 (NG75), and 1995 (NG95) at SJER (columns with different letters are significantly different [$P \leq .05$] by pairwise contrasts).

Livestock Concentration Activities

Any form of livestock concentration activity significantly increased soil bulk density (*fig. 4*), with supplemental feeding stations being the most compacted sites found in this study. These results reconfirm the importance of keeping livestock concentration sites as far from water bodies as possible to reduce the risk of elevated runoff levels from these sites reaching surface water.

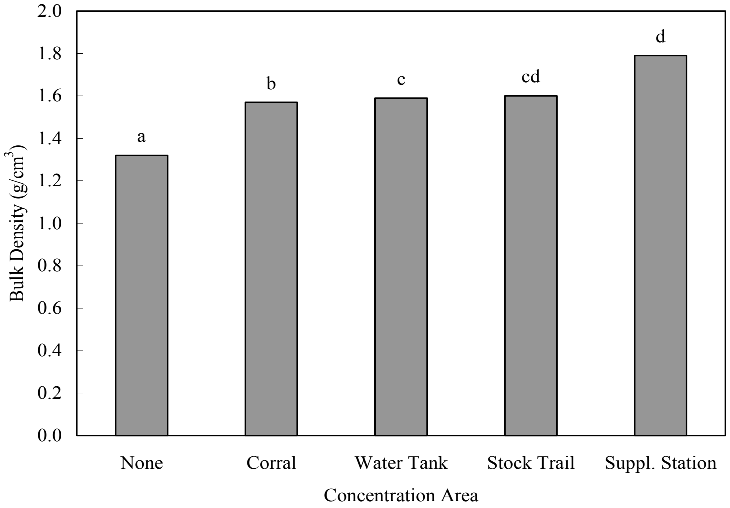

Figure 4—Mean soil-surface bulk density for areas without livestock concentration (none), corrals, water tanks, stock trails, and supplemental feeding stations at SJER (columns with different letters are significantly different [$P \leq .05$] by pairwise contrasts).

Conclusions

We found the presence or absence of oak tree canopy, grazing history, and livestock concentration areas significantly affect soil-surface bulk density on oak savanna rangelands at SJER. Soil-surface bulk density was 19 percent lower under oak canopy than in adjacent open grasslands. Livestock grazing at all levels found on SJER increased bulk density above areas excluded from grazing for 5, 25, and 65 years. There was no significant difference among the three exclosures, indicating that reversal of soil compaction from grazing on these sites occurs within 5 years. Areas with 15 years of light grazing (> 1,000 lb ac^{-1} RDM) had significantly lower bulk density than moderately (800-600 lb ac^{-1} RDM) and heavily (<400 lb ac^{-1}) grazed sites, which were not significantly different from each other. RDM recommendations at, or above, 800 lb ac^{-1} will likely lead to elevated soil-surface bulk density on these soil series. However, these results for soil-surface bulk density may not translate into an identical response in surface runoff to grazing history given the inherently high infiltration capacity of these sandy soils (Tate and others 2000). Further data collection will continue at SJER, enabling us to test for potential interactions between the effects of grazing history, canopy, and topographic position on bulk density.

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Historical Jigsaw Puzzles: Piecing Together the Understory of Garry Oak (*Quercus garryana*) Ecosystems and the Implications for Restoration[1]

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Abstract

Ecosystem restoration requires a set of reference vegetation conditions which are difficult to find for Garry oak *(Quercus garryana)* ecosystems in Canada because contemporary sites have been drastically altered. A survey of historical information provides only limited clues about the original understory vegetation. Although there is considerable variation in the soils, climate, and successional status of current ecosystems, an exploration of the ecology of contemporary, native grass species existing in association with Garry oaks can point to which species may have been adapted to the historical disturbance regimes of pre-European contact ecosystems. Both California oatgrass (*Danthonia californica*) and *Achnatherum* sp., such as Lemmon's needle grass (*Achnatherum lemmonii*), have ecological characteristics that suggest they are adapted to the disturbance regimes of fire and camas digging. These characteristics include dormancy, hygroscopic awns, and self-pollinated cleistogenes.

Introduction

Reference conditions are critical for defining restoration goals, determining the potential of restoration sites, and evaluating the success of restoration. This reference information is commonly derived from contemporary, undisturbed reference sites and/or historical data (White and Walker 1997). One of the challenges in deriving reference conditions for the Canadian range of Garry oak ecosystems is determining a target for herbaceous species composition, especially native grass species.

The Garry oak ecosystem is limited in Canada primarily to southeastern Vancouver Island as far north as Comox, BC and the southern Gulf Islands (Erickson 1993, GOERT 2001). Although Garry oak ecosystems stretch along the west coast of North America as far as southern California, the Canadian portion is geographically, genetically, and ecologically important because it occurs at the extreme northern limits of this distribution (GOERT 2001). It is also distinct because adjacent Garry oak ecosystems in Washington State tend to be located on glacial outwash soils (Dunn 1998, Dunn and Ewing 1997), whereas in British Columbia, oak ecosystems are primarily on rock balds or deeper soils (Roemer 2000).

Contemporary Garry oak ecosystems throughout their range are severely fragmented, have had drastic alterations to their ecological processes, and have been

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[1] An abbreviated version of this paper was presented at the Fifth Symposium on Oak Woodlands: Oaks in California's Changing Landscape, October 22-25, 2001, San Diego, California.

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heavily invaded by exotic species and woody native species (Fuchs 2000). This limits their ability to serve as reference sites. In Canada, the Garry oak ecosystem is one of the three most endangered ecosystems and has become so degraded that only one percent remains close to a natural state. The remaining patches are small and extremely fragmented (GOERT 2001, Hebda and Aikens 1993).

The Garry oak ecosystem has been invaded by exotic species to such a degree that 40-76 percent of the herbaceous species in meadows are exotic and exotic species dominate the herbaceous cover, ranging from 59-82 percent (Erickson 1996, Roemer 1995). The original species composition is difficult to determine given the high levels of invasion by exotic grass species and paucity of native perennial grasses remaining.

Large-scale processes have also been altered, most notably by fire suppression that began soon after European settlement. Regular fires kept meadows free from invasion by woody species and maintained rich food resources for Coast Salish First Nations (Lutz 1995). Native species that are dominant now may be favored by current regimes (e.g., fire suppression) which differ from the influences present in the original Garry oak ecosystems (Bartolome and Gemmill 1981, Dunwiddie 1997). In addition, contemporary camas harvest by First Nations is extremely limited.

Because of the degradation of existing remnants of Garry oak ecosystems and the fragmentation of patches, restoration is critical to improve functionality and connectivity of the ecosystem (GOERT 2001). However, restoration efforts have been seriously hindered by a lack of reference conditions.

The role of native grass species and their relative abundance compared to forbs before European contact is not known. If native grasses were prominent, identification of the former dominant species in the ecosystem is critical for defining reference conditions.

In order to complement the information from existing sites, I reviewed historical literature from explorers, land surveyors, and early settlers for clues to herbaceous species composition and disturbance regimes. To augment this limited information, I surveyed contemporary literature on the ecology of native grass species currently found in Garry oak ecosystems to pinpoint candidate species that might have been abundant in the putative original ecosystem. The species researched were blue wild-rye (*Elymus glaucus* ssp. *glaucus*), California oatgrass (*Danthonia californica*), California brome (*Bromus carinatus*), June grass (*Koeleria macrantha*), Alaska oniongrass (*Melica subulata*), Lemmon's needlegrass (*Achnatherum lemmonii*) and Roemer's fescue (*Festuca idahoensis* var. *roemeri*). Although the composition of Garry oak ecosystems is highly variable, the ecology of the species and their adaptive strategies can offer suggestions as to which species would have been favored under former disturbance regimes. This paper does not address experimental data but instead reviews historical and contemporary literature in order to highlight the possible original species composition and indicate where future research should be focused.

Methods and Materials

I examined historical writings from settlers, land surveyors and explorers for descriptions of Garry oak ecosystems, with particular focus on the herbaceous community. These documents were obtained from the British Columbia Archives, libraries at the University of British Columbia and the University of Victoria, the Cowichan Valley Archives, and the Royal British Columbia Museum.

I also reviewed current literature on native grass species now found in Garry oak ecosystems to determine the ecological characteristics of individual species, including their response to disturbance, production of cleistogamous seed, dormancy and hygroscopic awns. I used this information to deduce which species would have been most likely to be common under former conditions and disturbance regimes.

Results

Historical Information

The historical literature that mentions the herbaceous layer of Garry oak ecosystems tends to be descriptive but not specific. There are species lists of showy forbs, but there are no descriptions or names recorded for grass species.

Judging from the descriptions "park-like" and "work of art," the historical herbaceous layer must have contained many flowering species. Mayne (1862) writes: "I have never seen wildflowers elsewhere grow with the beauty and luxuriance they possess here."

Historical descriptions of the grass component of the ecosystem require greater interpretation than that of forbs. Given the focus on self-sufficiency of the new Hudson's Bay Company colony, grass for forage would have been of considerable interest to settlers. The first governor of Victoria, Sir James Douglas, described in 1842 the rich, moist bottoms around future Fort Victoria as having an "abundance of grass and several varieties of red clover" (Bowsfield 1979). Other early reports of grasses associated with oaks seem to confirm that grass and grass/forb complexes were common occurrences in historical oak ecosystems (Fitzgerald 1848, Anonymous 1849).

Fire was a common feature of the pre-European contact ecosystem. In places with regular burns, the "fire runs along the grass at a great pace and it is the custom here if you are caught to gallop right through it: the grass being short, the flames being little and you are through it in a second" (Anonymous 1849).

Another report describes "[an area] which had not a blade of grass growing, owing to it having lately been burnt by the Indians, and that a few months afterwards, on going over the same spot, …the grass up to his middle in height" (Fitzgerald 1848).

Although by the 1860s there are numerous references to "fertile, grassy pastures," it cannot be determined if these are composed of native or exotic species. Extensive early grazing was highly destructive but relatively short in duration (Lutz 1995). Overgrazing led to a scarcity of "natural grasses" which caused the importation and sowing of exotic range species as early as 1851 (Bowsfield 1979; Grant 1857). By 1859 "varieties of every grass species which grows in Europe, and many which do not, are found" (Mayne 1862). Although it seems clear that grasses were common in the putative original Garry oak ecosystem, there are no early descriptions of the grass species present.

Before European settlement, specific areas of Garry oak ecosystems were intensively managed by the Coast Salish people for food production. This subjected the soil to frequent mechanical disturbance. The camas beds were managed as follows: "where the camas grew thick, the women had their own plots marked off with stakes…. Women dug the bulbs in the spring… When they had finished they leveled the ground and covered it with seaweed. Later when it was dry, they burned it over" (Suttles 1987).

Contemporary Ecological Information

In the absence of concrete details on historical understories, contemporary ecological characteristics of native grasses can be used to infer which species would have been adapted to the historical disturbances of fire and digging. Species differ in response to these environmental conditions both in vegetative growth and in germination characteristics *(table 1).*

Table 1—*Adaptations to disturbance regimes of grass species associated with Garry oak ecosystems.*

	Vegetative response to fire	Dormancy	Cleistogenes	Hygroscopic awns
Blue wild-rye	High tolerance	No	No	No
California oatgrass	High tolerance	Yes	Yes	Yes
California brome	No data	No	Yes	No
June grass	High tolerance	No data	No	No
Alaska oniongrass	High tolerance	No	No	No
Lemmon's needlegrass	No data	Yes	Yes (*Achnatherum* sp.)	Yes (*Achnatherum* sp.)
Roemer's fescue	Decreases in cover	No	No	No

Vegetative Response to Disturbance

Native grass species differ in their response to fire. Blue wild-rye, Alaska oniongrass, June grass and California oatgrass have a high fire tolerance and do not decrease in cover with burns (FEIS 1999, Hatch and others 1999, USDA 1999). Idaho fescue (*Festuca idahoensis*) decreases in cover after burns, especially severe burns that damage the basal buds just below the soil surface (Dunwiddie 1997, FEIS 1999, Wikeem and Strang 1983). Few researchers have measured the response of these species to successive fires.

I could find no published information on the response of native grasses to indigenous harvesting regimes.The native species associated with Garry oak ecosystems are primarily bunchgrasses which do not spread extensively by rhizomes (Hitchcock 1969). With the combination of mechanical soil disturbance from camas harvesting and regular fires, recruitment from seed would have played an important role in determining species composition since patterns in plant succession are closely related to germination requirements and seedling establishment (Bartolome 1979).

Dormancy

One strategy that species use to adapt to disturbances is the formation of seedbanks by dormant seeds that require specific environmental cues to germinate.

Species that are adapted to establishing after a disturbance or in gaps generally make up the largest component of grassland seed banks (Rice 1989).

Many native species present in Garry oak ecosystems do not form seedbanks but germinate in the fall once rains begin. Idaho fescue (FEIS 1999, Young 1982), blue wild-rye (Archibald and others, 2000, Knapp and Rice 1994, Link 1993, Rose and others 1998), California brome (FEIS 1999, Link 1993, Rose and others 1998), and Alaska oniongrass (Rose and others 1998) germinate readily without the need for stratification.

Other species, including California oatgrass (Knapp and Rice 1994, Laude 1949, Trask and Pyke 1998), Lemmon's needle grass (Trask and Pyke 1998) and other *Achnatherum* sp. (Rose and others 1998), do not germinate in the fall and require specific treatments to overcome dormancy.

Cleistogenes

Cleistogenes are self-pollinated seeds that are produced from flowers that do not open. About 60 percent of species that produce cleistogenes are colonizers of disturbed or early successional habitats. Most of the non-ruderal species are "stress-tolerators," often found in sites with low moisture (Campbell and others 1983). Cleistogenes are often produced during stressful conditions, such as overgrazing or repeated mowing, and found in areas susceptible to fire (Campbell and others 1983, Clay 1983, Dobrenz and Beetle 1966).

California oat-grass can produce up to eight cleistogamous seeds per node in the leaf sheaths (25-36 per plant), often more seeds than are produced from cross fertilization (21-33) (Dobrenz and Beetle 1966, Hitchcock 1969). Some *Achnatherum* sp. also produce this type of cleistogene, although Lemmon's needlegrass is not specifically mentioned in the literature (Campbell and others 1983). Under light and moisture conditions adverse for flowering, California brome produces cleistogenes in the same panicle as cross-pollinated, chasmogenes, but the florets do not open due to lodicule failure (Campbell and others 1983).

Although other species in the same genera of those studied are known to produce cleistogamous seed (Campbell and others 1983), I could find no reference to cleistogenes for the species associated with Garry oak ecosystems.

Hygroscopic Awns

Hygroscopic awns cause seeds of some grass species in the genus *Danthonia* and *Achnatherum* to move along the soil surface until they lodge in a microsite and become buried in the soil (Peart 1979). Burial is especially important for the survival of grass seeds in fire-prone habitats. There are no references in the literature to hygroscopic awns of the other grass genera native to Garry oak ecosystems and examination of seed indicates they do not have them.

Discussion and Conclusion

The historical data concerning the understory composition of Garry oak ecosystems is sketchy at best. There is no detailed information regarding species composition and no descriptions of which grass species were present. The few descriptions of the grasses refer to waist-high grasses, although shorter grasses are also mentioned in connection with fire. However, from the historical writings it seems clear that grasses and grass/forb complexes were an important component of historical ecosystems. The historical literature clearly indicates that fire and soil disturbance from camas harvesting were common, at least in some areas.

The current Garry oak landscape is highly variable as a result of variation in many factors including soil depth and type, topography, disturbance history, slope, aspect and woody species cover. These factors must be incorporated into the establishment of reference conditions for restoration. Given the complexity of a landscape managed by fires and its mosaic affect, it is highly likely the ecosystem was variable before European contact. No single dominant species would have been consistent on the landscape scale. However, in sites that were more intensively managed by First Nations, the ecological adaptive strategies of some grass species indicate that they would have been more likely to occur than other species.

California oatgrass and Lemmon’s needlegrass are both candidate species for regularly disturbed ecosystems. Both have innate dormancy that may cause them to form persistent seedbanks. Both species produce cleistogenes and have hygroscopic awns that are known to be associated with disturbance-prone habitats. The lack of response of California oatgrass to fire reinforces the potential for it to have been a component of the original ecosystem. Fire response information for Lemmon’s needlegrass was not found. The potential for California oatgrass to be a dominant bunchgrass of the original Canadian Garry oak ecosystem is also reinforced by the likelihood that it was historically an important dominant in Californian coastal prairies (Hatch and others 1999), especially in drier areas (Hecktner and Foin 1977). California oatgrass, however, is considerably shorter (<0.5 m) than the historical references suggest with their descriptions of waist high grasses (Hitchcock 1969).

Native grasses will be foundation species for restoration efforts in Garry oak ecosystems (GOERT 2001). Native bunchgrasses create favorable sites for the establishment of other native species by reducing soil-surface temperatures and increasing nutrient availability. In grasslands, bunchgrasses may control the spatial distribution of species and their presence has been linked to increased species diversity (Hatch and others 1999). Native grasses play an important role in preventing invasion by exotic species because they provide soil cover during the winter months when many of the forb species are dormant. Although very little is known about the successional progression of herbaceous species in Garry oak ecosystems, it seems likely that native grasses and legumes would be the first to colonize open ground since many of the forbs take years to mature. Restoring native grass species is therefore critical for restoring the complexity and diversity of understory species.

Determining which species may have been present with pre-contact disturbance regimes is only the first step towards defining reference conditions for the herbaceous layer of these ecosystems. The long-term stability of reintroducing these species without re-establishing the disturbance regimes that helped foster them is questionable. This is further complicated by the presence of exotic species whose response to fire and other original disturbance regimes may impact restoration goals.

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Biodiversity of Mycorrhizas on Garry Oak (*Quercus garryana*) in a Southern Oregon Savanna[1]

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Abstract

Garry oak or Oregon white oak (*Quercus garryana*) is the dominant vegetation on the Whetstone Savanna in Jackson County, Oregon. The site is located on the western edge of the Agate Desert, an alluvial fan capped with shallow clay loam over a cemented hardpan. The landform exhibits patterned ground with mounds and vernal pools. The oaks are associated with buck brush (*Ceanothus cuneatus*) and with native and exotic grasses. In preparation for a study of the biocomplexity of common mycorrhizal networks among oaks and grasses, we examined the mycorrhizal morphotypes on Garry oak. We sampled soil cores at distances half way to the canopy edge, at the canopy edge, and outside the canopy and have identified over 40 ectomycorrhizal morphotypes including *Cenococcum geophilum*. Infection rates on oak roots were lowest on trees growing in or near vernal pools and highest on oaks growing in groves with closed canopies. Using the fungal specific primers ITS1-F and ITS4 and the restriction enzymes *HinfI* and *TaqI*, we amplified DNA via polymerase chain reaction (PCR) to compare ectomycorrhizal morphotypes. Small differences in mycorrhizal morphology correlated with differences in restriction fragment-length polymorphism (RFLP) patterns, suggesting that there were many different species. We also observed the unusual occurrence of endomycorrhizas with intraradical hyphae and vesicles in oak roots.

Introduction

Although the association of oaks with fungal fruiting bodies or mushrooms (Arora 1979) and mycorrhizal fungi are well known (Trappe 1962), the below-ground interactions of oaks and fungi receive less scientific attention. Another major inference is that the fleshy fungal fruiting bodies associated with oaks correlate with the fungi that form ectomycorrhizas on roots (Arora 1979). However, although both ectomycorrhizal fungi and fungal fruiting bodies associate with Garry oak (*Quercus garryana*), the two fungal forms correlate poorly. That is, the ectomycorrhizas appear to be different species from the mushrooms.

Some studies on inoculations of oak roots clearly identify the fungi involved in mycorrhizal formation. For example *Pisolithus tinctorius*, *Suillus granulatus*, *S. luteus*, *Thelephora terrestris*, and *Cenococcum geophilum* form ectomycorrhizas with *Q. robur*, black oak (*Q. velutina*), and eastern white oak (*Q. alba*) in culture (Dixon

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and others 1984). In culture, *P. tinctorius* and *Scleroderma auranteum* form ectomycorrhizas with red oak (Beckjord and others 1985). Neither of these studies described the morphotypes. At that time, methods for correlating DNA of ectomycorrhizas with that of inoculum were not available. Furthermore, there is little information whether the fungi used as inocula in culture form the major part of field inocula or whether they are common or rare morphotypes.

Many studies of ectomycorrhizas on oaks have not distinguished among morphotypes and hence did not enhance our understanding of systematic and functional biodiversity. Wasserman and others (1987) identified heavy metals in mycorrhizas of eastern white oak and red oak without regard for the species of oak or the ectomycorrhizal morphotypes. Brundrett and others (1990) examined the structure of ectomycorrhizas on three species of oaks, but did not document morphotypes. Berman and Bledsoe (1998) provided descriptions for nine morphotypes and photographs of six morphotypes, but no DNA information or taxonomic identification.

New methods to identify ectomycorrhizas have led to more precise descriptions, at first as morphotypes without certainty about taxonomic identification, more recently with comparative DNA analyses, and with DNA sequencing to identify fungi at various taxonomic levels (Bruns and others 1998). Standardized descriptions of ectomycorrhizal characteristics have facilitated comparisons of ectomycorrhizal morphotypes even without knowing the taxonomic identity of the fungus (Agerer 1987-1998, Agerer and others 1996, Goodman and others 1996). Amplification of mycorrhizal DNA by fungal-specific primers, followed by restriction digests, has added a central quantitative character to morphological descriptions so that one can ask whether two similar morphotypes are the same fungal species. Comparison of mycorrhizal restriction fragment-length polymorphisms (RFLPs) with fungal fruiting body RFLPs helps identify morphotypes. This allows us to correlate ectomycorrhizal fungi with fungal species.

Endomycorrhizas, a second major class of mycorrhizas found on herbs, forbs, and some tree species, occasionally have been reported on oaks: *Q. rubra* (Grand 1969), *Q. imbricaria* (Rothwell and others 1983), and *Q. agrifolia* (Egerton-Warburton and Allen 2001). These observations extend our understanding of the complex ecto- and endomycorrhizal support system for oaks.

No studies have addressed the diversity or distribution of ectomycorrhizal fungi on Garry oak (*Quercus garryana* Hook). In spite of interest in habitat, systematics, tree health, natural regeneration, and restoration of Garry oaks, no studies have gone below ground to see which fungal associates are present. For example, we do not know how much variability there is among oaks at different sites, nor do we know the effects of grazing, fire, or non-native grasses on mycorrhizas. In other oak species, ectomycorrhizas are influenced by light intensity and by soil factors including aeration, moisture, organic matter, pH, temperature, and fertility (Garrett and others 1979). Diversity data from ectomycorrhizas on a Garry oak savanna can provide an initial base for comparing other stand conditions. The purpose of our study was to describe the diversity of ectomycorrhizas on Garry oak roots.

Methods and Materials

Whetstone Savanna, a 58-ha Preserve owned by The Nature Conservancy, is located on the western edge of the Agate Desert in Jackson County, Oregon (42 degrees 25 minutes North latitude 122 degrees 54 minutes West longitude T365 RSW sec 23, 26). The Agate Desert, an alluvial fan capped with a shallow layer of clay loam over cemented hardpan, is characterized by patterned ground with mounds and vernal pools. This landform is not true desert as it receives 48 cm of precipitation annually. The Whetstone Savanna site supports a mix of scattered lone trees and denser groves of Garry oaks. Buck brush (*Ceanothus cuneatus*) grows adjacent to Garry oaks, but not under the canopy. The grassland understory of Garry oaks supports perennial native bunch grasses including Lemmon's needlegrass (*Achnatherum lemmonii*), California oatgrass (*Danthonia californica*), and many introduced annual grasses including medusa head (*Taeniatherum caput-medusae*) and several *Bromus* species. Whetstone Savanna has a recent history of cattle grazing and logging of Ponderosa pines. (Borgias 1994)

Soil samples were extracted with a soil corer (2.5-cm diameter by 15 cm) from under Garry oaks at edges of oak stands where tree canopies overlapped grasses, buckbrush or other Garry oaks. Soil samples were collected along 4 or 5 radii at three distances from the trunk: 0.5 x canopy, 1.0 x canopy, and 1.5 x canopy. Samples (8-20 per tree) were immersed in water over a 1.0-mm sieve. Ectomycorrhizal morphotypes were distinguished by macroscopic and microscopic characteristics (Goodman and others 1996).

For endomycorrhizas, roots were cleared in KOH, washed in NH_4OH and H_2O_2 to remove phenolic compounds, stained in Chlorazol Black E, and mounted in PVLG (Brundrett and others 1996). Digital pictures of macroscopic and microscopic root tip characters were taken with Spot RT color digital camera.

DNA was extracted from ectomycorrhizal tips following a CTAB protocol, and amplified via polymerase chain reaction (PCR) using the fungal-specific primers ITS1-F and ITS4 (Bruns and others 1998). The PCR product was cut with the restriction enzymes *HinfI* and *TaqI* (Bruns and Gardes 1993, Gardes and Bruns 1996). The PCR product and the restriction fragments were run on a 4 percent acrylamide gel. Gels were stained with ethidium bromide and photographed using a UV transilluminator and camera with Fotodyne imaging software. Gel analysis was done using ONE-Dscan software (ONE-Dscan 1998).

Results

Above ground we collected fruiting bodies of 39 fungal species located under or near oaks. Ten species were Ascomycetes of which five were hypogeous (fruiting below ground). The other 29 species were Basidiomycetes of which 24 were fleshy fungi likely to be mycorrhizal.

In two collecting seasons (1999, 2000), we found over 40 ectomycorrhizal morphotypes at one site on Garry oak roots in the upper 15 cm of mineral soil (Southworth and others 2001). Most morphotypes were found only once, but five *(figs. 1.1-1.5)* were found on 5 percent or more of trees. The most common extomycorrhizal morphotype was *Cenococcum geophilum* (SOU 3; *fig. 1.1*) that forms sclerotia, but not fruiting bodies. SOU9, SO12, SOU13, and SOU30, the other four morphotypes *(figs. 1.2-1.5)* are unidentified at present.

In addition to morphotyping, we used molecular methods to identify fungal species on roots by comparing RFLP patterns from mycorrhizal roots with RFLP patterns from fruiting bodies. We produced RFLPs from 28 ectomycorrhizal morphotypes and from 31 fungal fruiting bodies. The RFLP bands, derived from *HinfI* and *TaqI*, showed that only one ectomycorrhizal morphotype matched a fungal fruiting body: a "truffle-like" *Peziza* (Arora 1979).

In addition to ectomycorrhizas, oak roots formed endomycorrhizas *(fig. 1.6)* characterized by non-septate hyphae and vesicles. Arbuscules were not seen. We also observed dark septate hyphae associated with oak roots *(fig. 1.6)*. Dark septate endophytes were not organized as ectomycorrhizas into a mantle and Hartig net, but grew as individual hyphae over the root surface or between root cells.

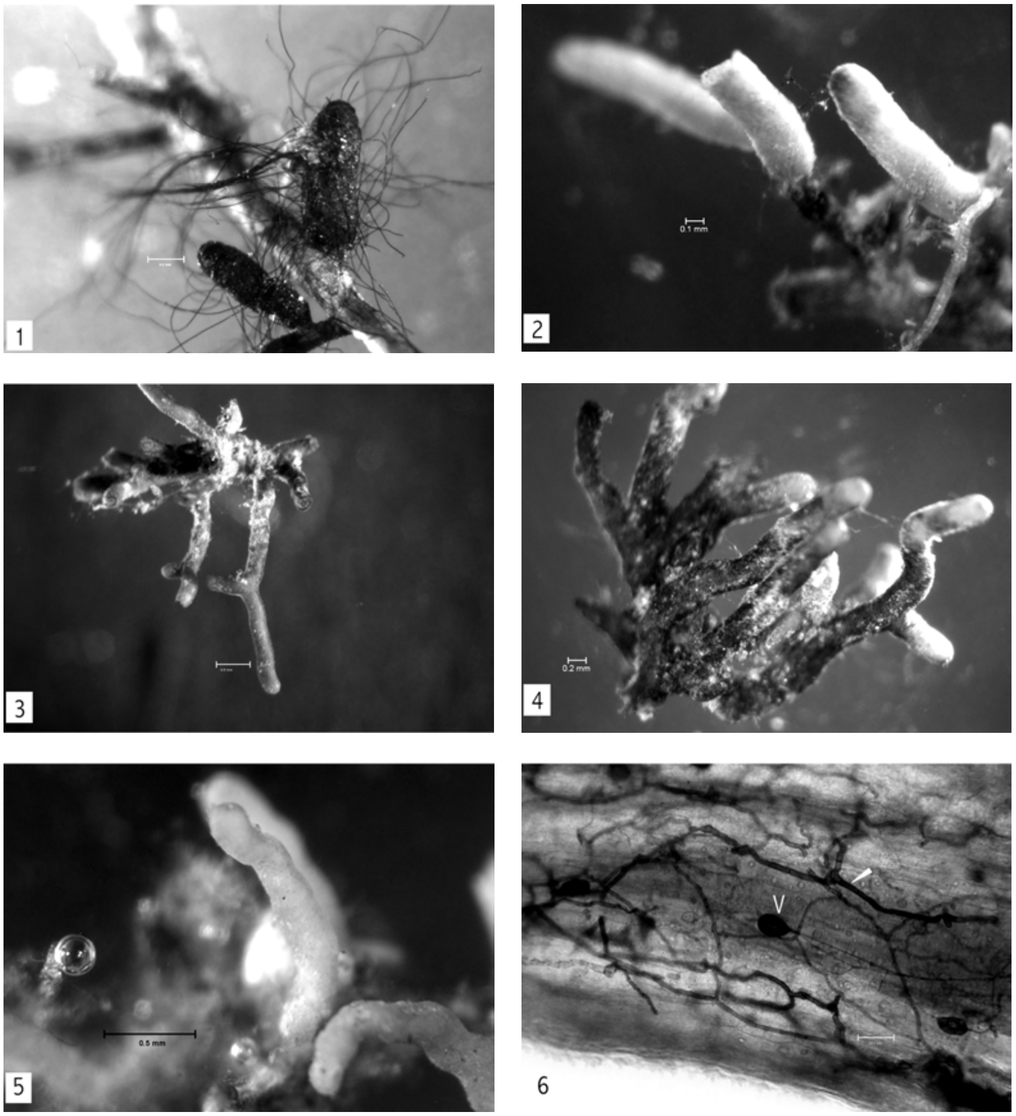

Figure 1—Ectomycorrhizal morphotypes on *Q. garryana* roots collected at Whetstone Savanna. **1.1)** *Cenococcum geophilum* (SOU3). Bar=0.2 mm. **1.2)** SOU9. Bar=0.1 mm. **1.3)** SOU12. Bar=0.5 mm. **1.4)** SOU13. Bar=0.2 mm. **1.5)** SOU30. Bar=0.5 mm. **1.6)** *Q. garryana* root with endomycorrhizal vesicles (V) attached to thin, non-septate hyphae. Branched dark-septate hyphae (arrowhead) are also present. Bar=25 μm.

Discussion

A large number of fungi form ectomycorrhizas with Garry oaks. It is likely that these differ in their physiological abilities such as nutrient uptake capacity. The result is an unrecognized complex of belowground components in Garry oak savannas.

The most abundant ectomycorrhizal morphotypes are leading candidates for participants in common mycorrhizal networks. *Cenococcum geophilum*, the most abundant ECM on roots of Garry oak, is ubiquitous and has low host specificity. These features may allow *C. geophilum* to play a key role in common mycorrhizal networks between plants. Endomycorrhizas are also potential participants in common mycorrhizal networks and may link oak networks to grass networks.

The disagreement in identity between ectomycorrhizal morphotypes and fruiting bodies may be explained in several ways. Mycorrhizal fungi may not produce fruiting bodies or may do so infrequently. Our sampling scheme may be too limited. We may need to take more mycorrhizal samples across the site and to sample more frequently and more exhaustively for fruiting bodies. Alternatively, not all fleshy fungi associated with oaks may form mycorrhizas; some fungi, “suspected” of being mycorrhizal, may in fact not be so.

Careful descriptions of ectomycorrhizal morphotypes can extend our ability to understand the mycorrhizal status of oak roots without knowing the identity of the actual fungus. If identification is important, we can apply PCR and RFLP methods that support classification of ectomycorrhizas and enable cross comparison of morphotypes as well as correlation with fungal fruiting bodies.

Conclusions

- The diversity of ectomycorrhizal morphotypes in a stand with one predominant tree species is remarkable.
- Species of fleshy fungi associated with oaks do not completely correspond to species of ectomycorrhizal fungi.
- Oaks form both ecto- and endomycorrhizas.
- Standardized descriptions of ectomycorrhizas provide a source of information about plant responses to environmental conditions.

Acknowledgments

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Invasive Perennial Grasses in *Quercus garryana* Meadows of Southwestern British Columbia: Prospects for Restoration[1]

Andrew MacDougall[2]

Abstract

Garry oak *(Quercus garryana)* meadows of the Pacific Northwest are heavily invaded but the dynamics surrounding this ecosystem transformation are poorly understood. Of particular uncertainty is the role of the invasive species in structuring the community, and the potential stability of this invasive-dominated system when disturbed. Clarifying such issues is central to restoration success for Garry oak meadows, one of Canada's most endangered terrestrial ecosystems. This paper examines the competitive inter-relationships among exotic and native flora, and how these inter-relationships are modified by a series of disturbance treatments (burning, mowing, and selective removal of invasives). Recruitment dynamics are also described. Pre-treatment surveys of vascular plant taxa identified 80 species within the study area located near Duncan, British Columbia, Canada. Thirty-nine of the species were non-native. Two of the invasives—Kentucky blue grass and orchard grass—were dominant, averaging a combined 80 percent of total cover in all plots. Disturbance treatments, regardless of type or intensity, caused significant decreases in total percent cover of the exotic dominant grasses, and significant increases in ground level light, total species richness, and total percent cover of native flora. A combination of disturbance and native seed additions revealed that native plant recruitment is limited by primarily by dispersal, though the dense invasive sward probably restricts recruitment success also. These results indicate that the invasive sward could be de-stabilized by disturbance treatments, though supplemental recruitment measures are also needed to restore native species dominance to these meadows.

Introduction

Plant invasions have transformed communities worldwide, changing fundamentally the composition, structure, and functioning of native floral assemblages (D'Antonio and Vitousek 1992, Mooney and Drake 1986). Of particular concern is the competitive displacement of native taxa by invading species. In the grasslands and oak savannas of western North America, displacement by exotic grasses approaches 100 percent in some areas (Harrison 1999, Heady 1977)

To restore invaded systems, we must understand how they function in their current state, and in particular, why the exotic invaders are so successful. Based on present-day dominance patterns in inundated plant communities, we tend to assume that the exotics are absolute competitive dominants. Compared to native flora, these species are better able to acquire limiting resources (e.g., light, soil moisture, soil nutrients, recruitment space) and over time displace native assemblages. And this

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[1] An abbreviated version of this paper was presented at the Fifth Symposium on Oak Woodlands: Oaks in California's Changing Landscape, October 22-25, 2001, San Diego, California.

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may be the case. But there is an alternative competition model that may explain present-day dominance patterns: contingent dominance. Rather than relying on outright competitive superiority, contingent dominance might be driven by historical disturbance events. For example, the combination of intense domestic grazing, fire suppression, and intentional introductions of massive amounts of Eurasian pasture grass seed could easily create a dominant and stable exotic assemblage that need not rely on relative competitive superiority. Or, exotic flora may be competitively dominant, but only because they are better adapted to contemporary human disturbance regimes. In undisturbed habitats, native flora may be competitive equals.

Determining the competitive relationships among exotic and native flora enhances our understanding of how biotic interactions shape community structure. But such assessments also guide restoration activity. Whether or not exotic flora are "absolute" or "contingent" dominants will determine the appropriateness of particular restoration measures. If exotic species are absolute competitive dominants, it is unlikely that they can ever be removed from the community. Restoration must focus on continued suppression of exotics to offset their competitive dominance over the native species (e.g., Weiss 1999). Alternatively, if present-day exotic dominance is driven by historical factors, rather than absolute competitive superiority, then restoration effort could focus on shifting current conditions, such as disturbance regimes, to favor other assemblage dominants (i.e., native flora). Given these possibilities, untangling competitive inter-relationships within invaded communities may be a critical step in effective restoration.

This paper seeks to describe existing competitive interactions within the heavily invaded Garry oak *(Quercus garryana)* meadows of southwestern British Columbia, and how these interactions are modified by disturbance. Plant invasions in this region occurred within a few decades following European colonization in the mid- to late 1800s and thus the processes that drove exotic inundation are no longer evident. However, by experimentally de-stabilizing and re-assembling this assemblage with disturbance and species-addition treatments respectively, we can begin to untangle the current role of the exotics within the community, as well as the potential for native species to once again become dominant. To explore these issues, I ask three questions based on the initial results (2 years) of a longer-term study: 1) What is the current species composition and relative species abundance of exotic and native flora within Garry oak meadows? 2) How are these factors transformed by varying types and intensities of disturbance (burning, mowing, selective removals)? and 3) How does disturbance affect the recruitment dynamics of native and exotic flora?

Methods

The study was conducted in the Cowichan Garry Oak Reserve near Duncan, British Columbia, Canada. The reserve is a 18 ha remnant of a highly fragmented oak meadow ecosystem extending along the coastal areas of southeastern Vancouver Island from Victoria to Courtney-Comox, and including many of the South Gulf Islands. Garry oak meadows in British Columbia contain approximately 350 vascular plant species, of which 139 are invasives (Fuchs 2000). Garry oak *(Quercus garryana)*, the most visible native species (hence the moniker "Garry oak meadows"), occurs at varying densities from sporadic to closed canopy. The most abundant ground flora species include small camas *(Camassia quamash)*, Henderson's shooting-star *(Dodecatheon hendersonii)*, long-stoloned sedge *(Carex* *inops)*, and Idaho fescue *(Festuca idahoensis)*. The most abundant exotics include Kentucky blue grass *(Poa pratensis)*, orchard grass *(Dactylis glomerata)*, and sweet vernal grass *(Anthoxanthum pusilum)*. The shrub Scotch broom *(Cytisus scoparius)* also dominates many sites (Fuchs 2000).

Two experiments were established in May 2000 at two locations within the Cowichan Reserve. The locations differed in soil depth (location A: soil >1 m deep; location B: soil depth 5-15 cm) to determine if treatment responses interacted with site factors. Oak meadow assemblages in British Columbia occur across a range of soil depths (from <1 cm to >1 m), which strongly determine relative native species abundances (Erickson 2002), and may also influence the type and intensity of invasion. In one experiment, focusing on the effects of disturbance treatments on species richness and abundance, 80 one m^2 plots were established in each of the two locations. Percent cover of all species was determined in May 2000 using a one m^2 frame divided into twenty “5 percent” cells. Four treatments were initiated in July 2000: control, burning, mowing, and selective removals of all exotic species. In October 2000, four additional treatments were implemented: control, autumn burning, autumn mowing, and autumn selective removals. The four July treatments were re-applied at this time also, for a total of eight treatments. Each of the eight treatments was replicated ten times per each location. Percent cover was re-assessed in May 2001. Beginning in July 2000, ground-level light levels (ratio of percent photosynthetically active radiation (PAR) above canopy vs. below-LiCor Quantum Sensor) and soil moisture (TDR 12 cm soil moisture probe) were measured every six weeks. Changes in total percent cover between May 2000 and May 2001 were compared for all identified species using t-tests for each treatment and for each location separately ($\alpha_{0.05/2}$). Percent PAR in April 1, 2001, a time when light availability is especially critical for seedling survival and vegetative growth of established individuals, was compared among treatments using a one-way ANOVA ($\alpha_{0.05/2}$). Soil moisture availability did not vary with treatment and is not discussed further.

In the second experiment, seedling recruitment was examined with and without burning, and with and without the experimental addition of native seed. Forty 0.6 m^2 plots were established in each of the two locations. Half of these plots were burned in July and October 2000. Seed from 13 native plant species was added to 20 of the 40 burned plots and 20 of the 40 unburned or control plots in October 2000 following the last burn. The number of established seedlings of all species, native and exotic, were tallied in late April and early May 2001.

Results

A total of 80 species were identified within the 160 plots at the two locations. Average species richness per plot was significantly higher ($t_{0.025,79} = 2.23$; $p<0.001$) at the shallow soil location (mean = 28 species) than at the deep soil site (mean = 19 species). Disturbance history apparently does not differ between these two locations, based on interviews with the long-term owner (age: 102 years) and supported by examination of air photos dating back to 1950. The deeper soil location also had fewer native plant species occupying significantly less percent cover ($t_{0.025,79} = 4.31$; $p<0.001$), suggesting that invasive plants have had a higher impact at this location. In addition, most the native plants in the deep soil site are considered habitat generalists rather than Garry oak meadows specialists in British Columbia (e.g., Sweet Cicely

(Osmorhiza chilensis)). The reverse was true for most of the native flora found on the shallow soil site (e.g., spring-gold *(Lomatium utriculatum)*, western buttercup *(Ranunculus occidentalis)*, Menzie's larkspur *(Delphinium menziesii)*, and prairie violet *(Viola praemorsa)*).

Significant treatment effects were detected for 21 of 29 species occurring at sufficient frequency to conduct a t-test. The remaining 51 species were rare, occurring typically in fewer than five of the 160 plots. However, treatment differences were not detected among any of the eight treatments except for the two controls (i.e., control vs. any of the disturbance treatments). This suggests that the most important effect of the disturbances initially was the removal of the exotic grass overstory and the exposure of bare soil, rather than any specific differences among the six disturbance types. The selective weeding plots did not differ in effect from the other disturbances and this is probably indicative of the low percent cover of native flora in many plots (typically <10 percent). It is unclear whether the lack of differences among treatments will remain consistent into the future or whether differences will develop in the subsequent years of this study. As a result of this lack of difference, the species response data for the disturbance plots were pooled.

For species showing significant responses to disturbance *(table 1)*, 16 are considered "increasers," demonstrating a significant increase in percent cover following the treatments in both locations. Nine of the 16 "increaser" species were native, and included both annual ruderal species and late-successional geophyte species (e.g., *Camassia quamash, Dodecatheon hendersonii*). Two of the native annual ruderals, two-colored Lupine *(Lupinus bicolor)* and small-flowered lotus *(Lotus micranthus)*, were not observed during the May 2000 census. Among the seven exotic "increaser" species, five were uncommon (≤2 percent mean cover) during the May 2000 surveys compared to the two dominant exotic species (Kentucky blue grass and orchard grass).

Four additional species had significant increases in one of the two locations only. Of note was sweet vernal grass, an exotic perennial grass that doubled in percent cover in response to the disturbances at the shallow soil location (10 percent to 22 percent). This species is considered a problematic invasive in other Garry oak meadow sites on southeastern Vancouver Island.

Only two of 29 species showed significant decreases in percent cover—Kentucky blue grass and orchard grass—though this was not consistent at both locations. At the deep soil location, Kentucky blue grass declined from 65 percent to 45 percent following the disturbances; it was the dominant species prior to perturbation. At the shallow soil site, where this species is less abundant (average cover = 26 percent), treatment responses were not significant. Orchard grass, the second most dominant species within the study area, decreased by 4-6 percent at both sites.

Six species showed no significant change after the disturbances, suggesting that they were slow to respond or were impervious to the perturbations. Two of these were native graminoids—California brome *(Bromus carinatus)* and blue wildrye *(Elymus glaucus)*.

Table 1—*Species responses (n = 29) between May 2000 and May 2001 within 120 one m*^{2} *plots from the deep-soil (Location A) and shallow-soil (Location B) sites. Values are percent cover per plot averaged for the 60 treatment plots per location (i.e., control comparisons not included). All treatment responses ("increasers," "decreasers") were significant using a t-test (*$\alpha_{0.05/2}$*). "Inconsistent change" species had different responses between the two sites.*

Response	Life form	Location A change	Location B change
Increaser species			
Camassia quamash	perennial forb	1.6 pct to 2.8 pct	5 pct to 10 pct
Dodecatheon hendersonii	perennial forb	does not occur	3.1 pct to 8.3 pct
Cardamine oligospora	annual forb	0 to 3.7 pct	0 to 1.5 pct
Cerastium arvense	perennial forb	does not occur	3.6 pct to 7.6 pct
Cytisus scoparius	perennial shrub	3.5 pct to 12.8 pct	0.7 pct to 3 pct
Larthyrus sphaerica[1]	annual forb	1.4 pct to 1.6 pct	4.7 pct to 8.1 pct
Lomatium utriculatum	perennial forb	does not occur	3.3 pct to 7.4 pct
Myosotis discolor[1]	annual forb	0.8 pct to 8.2 pct	0.1 pct to 1.1 pct
Ranunculs occidentalis	perennial forb	does not occur	2 pct to 6.9 pct
Sanicula crassicaulis	perennial forb	11.9 pct to 19.3 pct	5 pct to 12.8 pct
Trifolium dubium[1]	annual forb	0.1 pct to 3.1 pct	0.1 pct to 2.7 pct
Valerianella locusta[1]	annual forb	0.5 pct to 4.5 pct	1.3 pct to 8.4 pct
Veronica arvensis[1]	annual forb	0.04 pct to 0.25 pct	0.3 pct to 1 pct
Vicia hirsuta[1]	annual forb	2.1 pct to 4.4 pct	0.8 pct to 2.6 pct
Vicia sativa[1]	perennial forb	7.8 pct to 22.1 pct	7.7 pct to 11 pct
Viola praemorsa	perennial forb	does not occur	0.8 pct to 2.4 pct
Decreaser species			
Dactylis glomerata[1]	perennial graminoid	16.1 pct to 10.3 pct	22 pct to 17.6 pct
No change species			
Bromus carinatus	perennial graminoid	7.2 pct to 7.8 pct	10.46 pct to 11.01
Bromus mollis[1]	annual graminoid	0.9 pct to 0.4 pct	1.2 pct to 1.5 pct
Elymus glaucus	perennial graminoid	0.6 pct to 0.1 pct	0 to 1.13 pct
Gerainium molle[1]	annual forb	0.4 pct to 0.8 pct	1.2 pct to 2.7 pct
Rumex acetosella	perennial forb	does not occur	0.3 pct to 0.6 pct
Claytonia perfoliata	annual forb	0.4 pct to 0.6 pct	1 pct to 0.8 pct
Inconsistent change			
Anthoxanthum odoratum[1]	perennial graminoid	5.2 pct to 5.8 pct[2]	11.5 pct to 20.6 pct
Poa pratensis[1]	perennial graminoid	65.4 pct to 43.3 pct	27 pct to 27 pct[2]
Bromus sterilis[1]	annual graminoid	2.7 pct to 4.3 pct	6.4 pct to 4.6 pct
Carex inops	perennial graminoid	5.9 pct to 10.2 pct	2.4 pct to 2.3 pct[2]
Galium aparine	annual forb	2.5 pct to 2.3 pct[2]	9.8 pct to 22.58 pct

[1] Invasive species

[2] Changes not significant

Within each of the two site locations, light levels differed significantly only between control and non-control treatments; they did not differ among the disturbance conditions *(fig. 1)*. The biggest contrasts in ground-level light intensity occurred between the two locations. In the deep-soil plots (Location A), the percentage of full light ranged mostly between 1-2 percent in the control plots while in the shallow soil plots (Location B), light levels were between 3-6 percent. Among the six disturbance treatments, light-level increases were also much higher in the shallow soil plots.

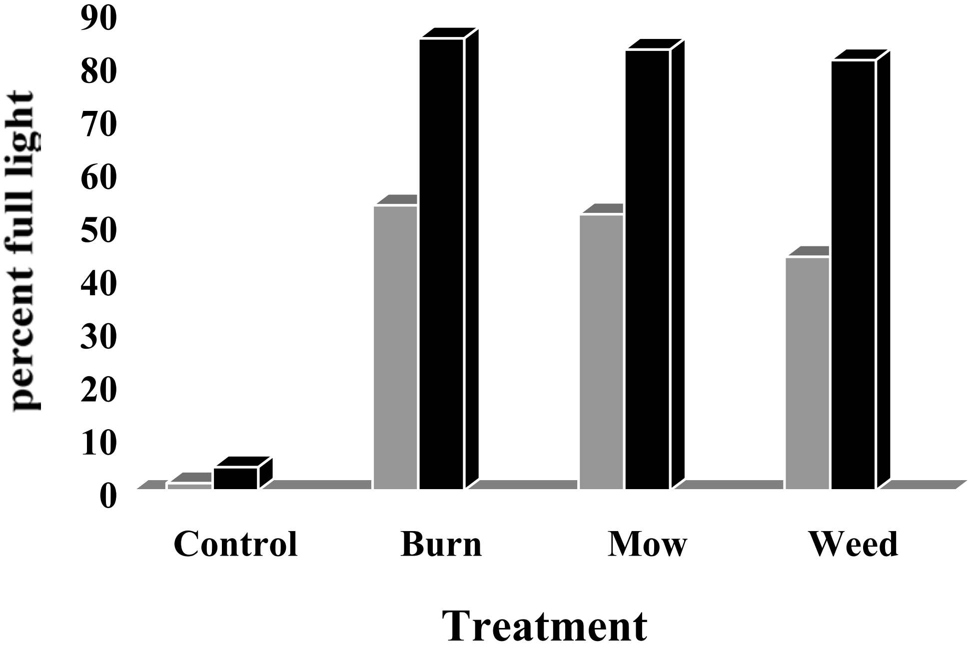

Figure 1—Percentage of full light among the disturbance treatments for April 2001; disturbances were last implemented in October 2000. Gray columns = deep-soil site (Location A); black columns = shallow-soil site (Location B). Derived from 160 one-m^2 plots. The burn, mow, and weed columns are the combination of summer and fall treatment response data, which did not differ significantly.

Seedling recruitment patterns were influenced significantly by both disturbance (fire) and the experimental introduction of native seed *(fig. 2)*. Under control conditions (unburned, no native seed additions) where exotic grass swards are dense, only 12 of 1,479 (n = 20 plots) of the recruiting individuals were native species. Burning alone increased the number of recruiting individuals, but it was mostly by exotic species that dispersed into the plot or were in the seed bank. Only 83 native species individuals (of 4,278 total individuals) established. Seedling establishment by experimentally introduced native seed was surprisingly high in both burned and unburned plots, suggesting that germination is not fully inhibited by the exotic sward.

Nonetheless, recruitment was highest for all species, native and invasive, in burned plots. Survival of these established native seedlings will be monitored in subsequent years of this study.

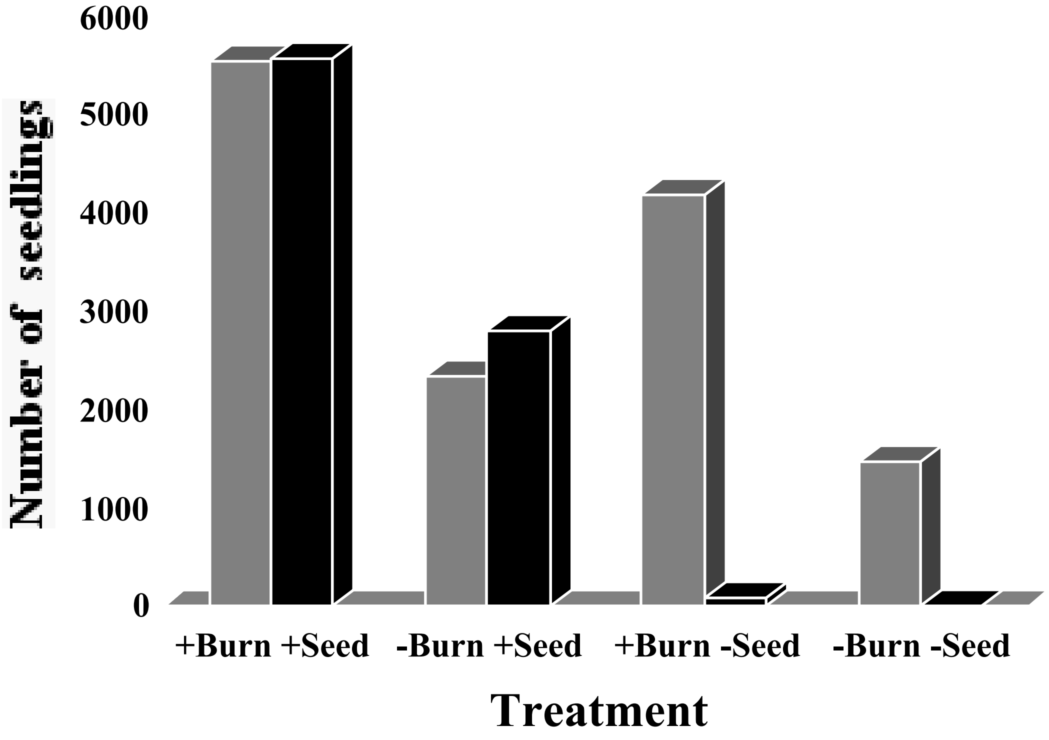

Figure 2—Total number of established seedlings (gray = exotic species; black = native species) within forty 0.60 m^2 plots. Treatments are 1) burned and native seed added (+Burn +Seed), 2) unburned and native seed added (–Burn +Seed), 3) burned and no native seed added (+Burn –Seed), and 4) unburned and no native seed added (i.e., control).

Discussion

Current abundance patterns within the Cowichan Reserve, one of the best remaining Garry oak meadows in Canada, are dominated by invasive flora, mostly the perennial grasses Kentucky blue grass and orchard grass. In the absence of disturbance, these two species form a dense sward of live material and litter that cover over 80 percent of the ground area in all study plots combined, and reduce ground light levels below five percent full light on average. All other species within the study area, invasive or native, are rare by comparison; few exceed 5 percent ground cover. Of the remaining invasives, most are small annual forbs (<15 cm height) or a mixture of annual and perennial grasses restricted mostly to drier shallow-soil sites (e.g., sweet vernal grass, annual *Bromus* spp., annual *Vulpia* spp., annual *Aira* spp.).

Patches of native ground flora are common in the reserve but occur typically in areas with shallow soil. Most abundant are spring-flowering geophyte species (small camas, great camas, Henderson's shooting star, spring-gold, and western buttercup) and various graminoids (California brome grass, blue wildrye, long-stoloned sedge, and Alaskan onion-grass *(Melica subulata)*). The grasses *Danthonia californica* and *Festuca idahoensis* are both very rare on the reserve, but do occur in abundance in nearby (<3 km) upper-slope and ridge-top remnant patches where solar exposure is high and soils are especially thin (<5 cm). Within the reserve, the apparent restriction of native species to drier micro-sites suggests that such assemblages are more resistant to invasion at these locations (i.e., competitively dominant), or that they are better able to tolerate summer moisture restrictions compared to Kentucky blue grass and orchard grass (i.e., competitive refuge). While the number of exotic species is higher on shallow soil sites compared to deep soil sites, these species rarely occur in abundance.

Disturbance treatments, regardless of type (burning, mowing, selective removals) or intensity (one or twice per year), all produced a similar response: a significant drop in percent cover of the dominant invasive grasses (except for Kentucky blue grass at Location B), and significant increases in ground level light, total species richness per plot, and total percent cover of established native flora. These responses suggest a suppressive effect of the exotic dominant grasses on other species. If we assume that the two grasses are able to continually regenerate within the dense sward, probably by vegetative spread rather than seed recruitment, then this assemblage would presumably be highly stable over time unless disturbed. Given that the Cowichan Garry Oak Reserve has not been actively grazed since the 1940s, this has probably been the case. Such suppressive dominance by a small number of grass species has been observed repeatedly in other ecosystems, including the tall grass and mixed-grass prairies of central North America (Collins 1987, Turner and others 1993). In these other systems, the dominance and stability of the grasses is perpetuated by their control of the surrounding micro-environment. Not only is ground-level light attenuated, but soil nutrient dynamics (e.g., increased carbon-nitrogen ratios) and soil moisture availability are also transformed compared to pre-invasion conditions. The restoration of these systems depends on breaking the control of dominant species with a range of disturbance treatments (e.g., grazing, burning, mowing), a finding that will likely apply to the Garry oak meadows.

The results of the recruitment treatments confirmed the suppressive effects of the dominant grasses: seedling establishment was highest when plots were disturbed. However, the data suggest that dispersal limitation may be even more restricting for native flora. Without the experimental introduction of native seed, native plant recruitment was close to nil, even within burned plots. Conversely, when seed was added to unburned plots dominated by the dense exotic sward, germination and initial establishment levels were high. While the survival of these germinants over time has yet to be determined, and may be extremely low, it suggests that dispersal inability is severely restricting native species' population spread within this exotic-dominated remnant. Given that the Cowichan Garry Oak Reserve contains large populations of native forbs which probably produce hundreds of thousands of seeds per year, this dispersal inability leads to questions regarding the long-term persistence of native flora. Or, at best, it suggests that species may only be replacing themselves in sites where they remain abundant, and they would be unable to re-colonize areas where native species have been eliminated. If this is the case, it highlights the need to protect remaining sites containing native plants, and to actively restore degraded remnants via seed and seedling introductions combined with exotic species control.

Conclusion

Results from this study, derived from the initial two years of a longer-term project, demonstrate the suppressive effect of dominant grasses within the Cowichan Garry Oak Reserve on Vancouver Island. It suggests that conservation management effects must focus on both disturbance treatments and recruitment supplementation to restore degraded oak meadow remnants. What remains unclear, however, is the longer-term prospects for re-establishing native ground assemblages that are not only dominant in species richness and percent cover, but are also resistant to re-invasion by exotics. If the exotic grasses are “absolute” competitive dominants, we will expect them to recover eventually from any and all disturbance applications and once again dominate. If this is true, then restorative efforts must focus on the continual suppression of Kentucky blue grass and orchard grass to reduce their suppressive impact on native flora. If the exotics are not absolute dominants, however, but instead have relied on a combination of European management practices and an absence of recent grazing to dominate (i.e., “contingent” dominance), then the re-establishment of a dominant and stable native assemblage could occur. Based on the initial results of this study, this later competitive model may be in effect. The percent cover of exotic dominants has dropped after only one year of treatments, and many native geophytes have doubled in percent cover. Given that many of these natives, especially small and great camas, can form dense and light-suppressing vegetation layers in a similar fashion as the invasive perennial grasses, it may be possible for native-dominated assemblages to resist re-invasion. Future efforts of this study will attempt to determine if such a development can occur.

Acknowledgments

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Does Habitat Matter in an Urbanized Landscape? The Birds of the Garry Oak *(Quercus garryana*) Ecosystem of Southeastern Vancouver Island[1]

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Abstract

Garry oak (*Quercus garryana*) was once a dominant habitat type on southeastern Vancouver Island, British Columbia but urbanization has severely fragmented and reduced its occurrence. This study tests whether bird abundance in remnant patches of Garry oak and adjacent Douglas-fir (*Pseudotsuga menziesii*) is related to Garry oak volume, patch size or urbanization. Breeding bird populations were surveyed at seven Garry oak sites and four adjacent Douglas-fir sites. Relationships between environmental variables and abundance of 17 species of birds were inferred by selecting the best linear regression model by Akaike Information Criterion. For five species, the best model included Garry oak volume, two species being positively related to oak habitat and three species preferring Douglas-fir habitat. Eight species were associated more with patch size or level of urbanization in the surrounding landscape. For these species, the effects of fragmentation overwhelmed the importance of habitat differences. While habitat degradation of remnant patches is a conservation issue, the bird community of this urbanizing landscape would most benefit if human modification of the surrounding landscape was reduced.

Introduction

Southeastern Vancouver Island, British Columbia, is an urban region with two dominant terrestrial ecosystems: Garry oak (*Quercus garryana*) parkland and Douglas-fir (*Pseudotsuga menziesii*) forest. Each provides different resources to wildlife and is expected to support different wildlife communities. The Garry oak ecosystem, for example, has an open canopy of Garry oak with a grassy understory (Erickson 1996). Douglas-fir dominated forest, on the other hand, has a closed canopy. Grass is nearly absent from the understory, which is dominated by salal (*Gaultheria shallon*) and sword fern (*Polystichum munitum*) (Feldman, personal observation).

The Garry oak ecosystem is considered endangered and there are many at-risk flora and fauna associated with Garry oak habitat (Erickson 1993). The major threats

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to the Garry oak ecosystem are habitat loss, fragmentation and invasion by exotic species. The center of British Columbia's Garry oak is located in what is now the city of Victoria. The greater area has a population of 304,287 and is growing at an annual rate of 5.7 percent (Statistics Canada 1999). Estimates put Garry oak ecosystem loss at between 95 percent and 99 percent since European colonization of the area (Hebda 1993). Consequently, Garry oak habitat is limited to small, remnant patches often surrounded by development.

This study uses the Garry oak ecosystem to test whether the unique habitat features of an ecosystem matter to birds in the face of extensive urbanization. This is done by comparing the abundances of bird species between Garry oak and Douglas-fir fragments of varying sizes and of varying land-use contexts. If habitat matters, then abundance should be related to habitat type instead of landscape factors. If urbanization is too extensive, patch size or level of urbanization in the landscape instead shapes site selection. In addition, we test whether Douglas-fir patches surrounding Garry oak have an influence on bird population size within Garry oak. A positive relationship indicates that Douglas-fir patches can act as a buffer to urbanization.

Methodology

Study Sites and Experimental Design

We used the Sensitive Ecosystem Inventory (Canadian Wildlife Service 1997) to select sites with the following criteria: 1) patches classified as being dominated by Garry oak; 2) patches larger than 4 ha, and 3) sites that are easily accessible. This resulted in the selection of seven sites along an urban-rural gradient emanating from the core of Victoria *(fig. 1)*. Sites differed in size and level of development in the surrounding landscape as measured by human population density *(table 1)*. Four of the seven Garry oak sites were surrounded by Douglas-fir forest, while three were surrounded by residential development. Bird communities were surveyed in Garry oak and Douglas-fir habitat patches.

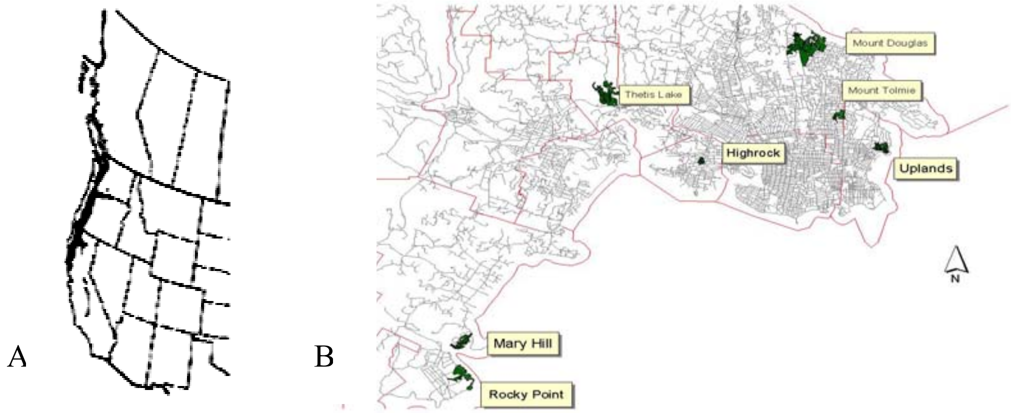

Figure 1—The study area: A) The Garry oak ecosystem (darkened area) ranges from California to British Columbia. B) Seven Garry oak patches were chosen for this project. Rocky Point, Mary Hill, Thetis Lake and Mt. Douglas patches were adjacent to Douglas-fir forest, while the remaining three were completely surrounded by city. Bird surveys were conducted in both the Garry oak and Douglas-fir habitats.

Table 1—*Environmental characteristics of each site.*

Site	**Garry oak volume (m^3/ha)**		**Patch size (ha)**		**Human population density (/km^2)**
Habitat type →	Garry oak	Douglas-fir	Garry oak	Douglas-fir	
Mount Douglas	34.76	0	21.21	52.6	1,041.87
Mary Hill	107.31	6.41	9.85	120.57	302.11
Rocky Point	285.31	3.37	9.40	22.25	302.11
Thetis Lake	17.47	1.45	6.56	44.56	545.13
Highrock Cairn	17.19	-	6.60	-	2,809.36
Mount Tolmie	24.42	-	17.97	-	2,344.88
Uplands	31.52	-	23.03	-	1,054.24

Bird Surveys

At each site, bird surveys were conducted along two parallel transects separated by 100 m. The transects were placed to maximize the length of the patch while avoiding edges. All transects were 400 m in length except Rocky Point and the Douglas-fir portion of Mount Douglas (350 m) and Highrock (250 m). Bird survey points were placed every 50 m along the transect.

Bird surveys were conducted between dawn and three hours after dawn from 5 May to 30 June 2000. During the survey, the observer walked the transect (starting point randomized) and stopped at each observation point. All birds seen and heard in 5 min. within a 50-m radius of the point were recorded on a map of the site. Five visits were made to Mary Hill, Rocky Point, Mount Douglas and Thetis Lake, while the remaining sites were visited four times. Visits to the same site were separated by at least five days.

Upon completion of the breeding surveys, the number of territories for each species at each site was determined by finding clusters of at least two observations from separate survey dates in approximately the same location on the map (i.e. territory-mapping method; Bibby and others 1992). The number of territories for each species was converted to a density value by dividing by the area surveyed. Of all the birds recorded, selected species were used in analyses based on: 1) appropriateness of the territory mapping method as an indicator of abundance (flocking species excluded), 2) frequency of occurrence (birds in fewer than five patches excluded), and 3) expected habitat relationship. The latter requirement was used to separate generalist species from those that are likely to differ in abundance between Garry oak and Douglas-fir habitat. Habitat use was derived from a study of Oregon's Garry oak and conifer habitats (Anderson 1972) and a study comparing grassland, open patches and Douglas-fir forests in the interior of BC (Schwab and Sinclair 1994). Seventeen species were used to make inferences regarding avian habitat selection. Based on the literature, nine species were expected to be relatively more abundant in Garry oak habitat, while eight species were expected to be associated with Douglas-fir patches. Overall species richness among sites was also analyzed for its relationship with the environmental variables.

Environmental Measures

Tree measurements were made along 50-m transects that ran perpendicular to the bird survey transects at each bird survey point. All oaks greater than 2 m in height and 5 cm in diameter within 5 m of each side of the transect were counted. Diameter at breast height and height were measured on five randomly chosen individuals.

Stem volume of Garry oak per hectare was determined in each site. This volume measure combines height and diameter at breast height via the following equation, developed for bigleaf maple trees (B.C. Forest Service 1983):

$$\log \text{volume} = -4.536696 + 1.907850 \log \text{diameter} + 1.120160 \log \text{height}$$

This measure was determined for each oak surveyed, averaged and multiplied by tree density to obtain a volume/ha measurement for each site. Stem volume was a surrogate for habitat type. Douglas-fir patches were expected to have little or no Garry oak.

Patch size was taken from the Sensitive Ecosystem Inventory GIS database (Canadian Wildlife Service 1997). The area of all the continuous polygons of one habitat type (Garry oak or Douglas-fir) were summed to derive overall patch area. Douglas-fir patch size was also used as the measure of buffer size since these patches surrounded Garry oak patches.

The 1996 Canada census was used to assess the human population in the census tract in which each site was located (Statistics Canada 1999). Since census tract area varied, population was divided by area to obtain a density measurement.

Data Analysis

The ultimate goal of this project was to make inferences regarding how the pattern of abundance of different species found in remnant patches related to variation in habitat and landscape factors. We developed a series of linear regression models consisting of one or more predictor variables: Garry oak volume, patch size, Douglas-fir buffer size, and human population density. In addition, we included a null model that relates a species' abundance to its mean and variance and describes the situation in which no discernable pattern in abundance is found.

The series of models represent multiple research hypotheses. For each species and overall species richness, the models are ranked based on how well each approximates the pattern in bird abundance data. The criterion for ranking is the Akaike Information Criterion (AIC; Burnham and Anderson 1998). Due to low sample size, an AIC variant, AICc, was used as the final measure. AIC/AICc is an objective way of finding the most parsimonious model of the pattern of bird abundance across fragments, given the parameters measured (Burnham and Anderson 1998). The model used for inferring a bird abundance-environmental variable relationship was most often the model with the lowest AICc (i.e. $\Delta = 0$, where Δ is the difference between a model's AICc and the lowest AICc). However, due to model selection uncertainty (i.e., the confidence that the model would be chosen with other data sets generated under the same conditions), model weighting and parameter importance (expressed as the sum of weights of models in which the variable appears) were also used to select the final model (Burnham and Anderson 1998). The above procedure was conducted on each of the 17 species and for species richness.

Results

Table 2 details the three best approximating models for each species and for species richness. For most species the model with the least AICc was used for inference. For brown-headed cowbird and northern flicker, however, model selection uncertainty was high and more than one model could be used for inference (i.e., $\Delta<1.0$). In these cases, the most parsimonious model with the most important variable was chosen as the best model.

Of the 18 final models, only three involved more than one environmental variable *(table 2).* Two species responded positively to oak volume, while three showed preferences for Douglas-fir habitat. Seven species chose territories irrespective of habitat type and were more affected by patch size or level of urbanization. For two species, the house wren (*Troglodytes aedon*) and Wilson's warbler (*Wilsonia pusilla*), each single variable model performed equally as well. Consequently, one final model could not be used for inference. The null model was the best approximating model for Bewick's wren (*Thryomanes bewickii*), spotted towhee (*Pipilo maculatus*), pacific-slope flycatcher (*Empidonax dificilis*), and overall species richness. Territory density of these species and species richness across fragments was random and could best be explained by population mean and variance.

Table 2—*The top 3 linear regression models relating bird territory density to environmental variables as chosen by AICc. Terms used in the final model have a positive (+) or negative (-) relationship with bird territory density.*

Best approximating models	K^1	AICc	ΔAICc	weight	parameter importance	relationship
<u>Anna's hummingbird</u>						
human pop. density	3	-28.95	0	0.23	0.55	-
area + human pop. density	4	-27.13	1.82	0.09		
area	3	-27.01	1.94	0.09		
<u>Bewick's wren</u>						
null	2	-13.93	0	0.33		
oakvol + human pop density	4	-11.93	2.00	0.12		
human pop density	3	-11.77	2.16	0.11		
<u>brown-headed cowbird</u>						
oakvol + doug. fir + human pop density	5	-27.04	0	0.26	oakvol 0.98	
oakvol	3	-26.84	0.20	0.24		+
oakvol + doug. fir	4	-26.45	0.59	0.20		
<u>brown creeper</u>						
oakvol	3	-16.47	0	0.25	0.47	-
oakvol + area	4	-16.24	0.23	0.22		
area	3	-15.93	0.54	0.19		
<u>chestnut-backed chickadee</u>						
human pop density	3	-24.11	0	0.46	0.60	-
oakvol	3	-22.49	1.62	0.21		
area + human pop. density	4	-21.66	2.45	0.14		
<u>chipping sparrow</u>	4					
oakvol + doug. fir	4	-48.46	0	0.41	0.59	oakvol + doug. fir +

Table 2 continued

Best approximating models	**K**[1]	**AICc**	**ΔAICc**	**weight**	**parameter importance**	**relationship**
oakvol + doug. fir + human pop. density	5	-46.90	1.56	0.19		
doug. fir	3	-46.32	2.15	0.14		
<u>dark-eyed junco</u>						
human pop. density	3	-21.02	0	0.53	0.73	-
area + human pop. density	4	-19.00	2.02	0.19		
null	2	-17.36	3.66	0.09		
<u>golden-crowned kinglet</u>						
oakvol	3	-17.71	0	0.42	0.54	-
null	2	-15.64	2.07	0.15		
human pop. density	3	-15.30	2.40	0.13		
<u>house wren</u>[2]	4					
doug. fir	3	-30.51	0	0.19	0.43	+
human pop. density	3	-30.14	0.37	0.16	0.41	-
area	3	-29.68	0.83	0.12	0.35	-
oakvol	3	-29.28	1.22	0.10	0.30	+
<u>northern flicker</u>						
oakvol + area + human pop. density	5	-45.41	0	0.42	oakvol 0.44 area 0.96 human 0.96	
area + human pop. density	4	-45.33	0.08	0.40		area – human -
area + doug. fir + human pop. density	5	-42.86	2.55	0.12		
<u>orange-crowned warbler</u>	4					
doug. fir + human pop. density	4	-23.53	0	0.26	0.37	doug. fir + human -
area + doug. Fir	4	-22.52	1.01	0.16		
area + doug. fir + human pop. density	5	-21.83	1.69	0.11		
<u>pacific-slope flycatcher</u>						
null	2	-11.58	0	0.83		
oakvol	3	-6.09	5.49	0.05		
human pop. density	3	-5.99	5.59	0.05		
<u>red-breasted nuthatch</u>						
area	3	-44.43	0	0.48	0.96	+
area + human pop. density	4	-43.43	1.00	0.29		
oakvol + area	4	-42.54	1.89	0.19		
<u>spotted towhee</u>	4					
null	2	-6.31	0	0.25		
human pop. density	3	-6.22	0.09	0.24	0.64	
area + human pop. density	4	-4.68	1.63	0.11		
<u>Townsend's warbler</u>						
human pop. density	3	-29.28	0	0.67	0.87	-
area + human pop. density	4	-26.92	2.35	0.21		

Table 2 continued

Best approximating models	K[1]	AICc	ΔAICc	weight	parameter importance	relationship
oakvol	3	-24.37	4.91	0.06		
Wilson's warbler[2]	4					
doug. fir	3	-25.83	0	0.20	0.45	+
oakvol	3	-25.26	0.57	0.15	0.36	+
human pop. density	3	-24.82	1.01	0.12	0.31	-
area	3	-24.71	1.12	0.11	0.34	+
winter wren						
oakvol	3	-14.41	0	0.34	0.48	-
null	2	-13.73	0.68	0.25		
area	3	-12.68	1.73	0.15		
species richness						
null	2	20.32	0	1		
human pop. density	3	65.56	45.24	1.5E-10		
oakvol + human pop. density	4	67.93	47.61	4.59E-11		

[1] Number of parameters.

[2] These species have four equally likely single variable models. A final model could not be chosen for inference.

Discussion

Only two species favour Garry oak habitat over Douglas-fir forest. The brown-headed cowbird (*Molothrus ater*) is avoiding the closed-canopy forest and selecting for oak habitat. The chipping sparrow (*Spizella passerina*) is also selecting for Garry oak habitat. Unlike the cowbird, it is restricted to those oak patches surrounded by Douglas-fir forest, thus showing a response to surrounding habitat. The chipping sparrow may be the only species for which the Garry oak ecosystem is a vital component for its persistence in the region. Further studies on chipping sparrow use and productivity in other open-habitats are needed to test this claim.

Although a community of oak-associated species is not currently present, a small Douglas-fir forest community existed. Three species (winter wren [*Troglodytes troglodytes*], brown creeper [*Certhia americana*] and golden-crowned kinglet [*Regulus satrapa*]) showed preference for Douglas-fir forest patches. These species are associated with conifer forests in other Pacific Northwest landscapes (Anderson 1972, McGarrigal and McComb 1995, Schwab and Sinclair 1994).

Urbanization factors, rather than patch type, were related to population size for the majority of the species analyzed. The red-breasted nuthatch (*Sitta canadensis*) and northern flicker (*Colaptes auratus*) had population size best modeled by the patch size variable. The former was limited to larger patches, while the flicker had higher populations in smaller patches. That so few species responded to patch size is surprising. Patch area was shown to be the largest influence on species richness and population size of over half of the species studied in other urbanized and fragmented woodlands (Blake and Karr 1987, Tilghman 1987).

Human population density—an indicator of urbanization in the landscape—was correlated to population size for five species (orange-crowned warbler [*Vermivora celata*], chestnut-backed chickadee [*Parus rufescens*], dark-eyed junco [*Junco hyemalis*], Townsend's warbler [*Dendroica townsendi*] and Anna's hummingbird

[*Calypte anna*]). Since four of these species are absent or in low numbers from highly urbanized patches, further urbanization of southeastern Vancouver Island may negatively impact these species. Even if loss of habitat itself is minimal, changes to the landscape surrounding Garry oak and Douglas-fir patches will introduce new predators, create hard edges and disrupt population processes such as immigration and dispersal (Saunders and others 1991). The influence of the surrounding landscape on populations within patches has been shown in other studies, including one from oak woodlands in California (Sisk and others 1997).

Management Implications

For most species, resource differences in Garry oak and Douglas-fir habitat are not reflected in population size. It is when the landscape around these patches becomes degraded that the habitat loses its value. Therefore, the most important management activity to maintain healthy bird communities is to minimize development around the patches. Site-level management would have some value. For example, maintaining open-oak habitat may benefit chipping sparrow. Preventing further habitat loss by restoring and conserving all remnants should be the priority for ensuring population persistence of southeastern Vancouver Island's birds. Considering that most birds in the region use both Garry oak and Douglas-fir habitat, these ecosystems should be managed together at the landscape scale.

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Environmental Relationships of Native Garry Oak (*Quercus garryana*) Communities at Their Northern Margin[1]

Wayne R. Erickson[2]

Abstract

Knowledge of relationships among plant communities and environmental variables can be used in restoration, ecological assessments, predictive mapping and conservation planning. This information would be particularly important in the conservation of endangered ecosystems, such as those of Garry oak in British Columbia. To investigate relationships, sixteen environmental variables were examined for a plant community framework using Detrended Correspondence Analysis and interpretive graphing. Overall, the variables and the degree of differentiation were adequately represented by the framework of 26 native communities. Most of the environmental multivariate space from DCA was covered by the communities, but not all communities were associated with variables. Fifteen communities were distinct, and many of the remaining eleven had special circumstances. Thirteen of the variables were associated with particular communities, a total of 26 times. Most important were site mineral soil exposure, soil coarse fragments and geographic area. The results could be used to develop environmental keys to plant community sites for practical field application.

Introduction

Garry oak (*Quercus garryana* Dougl.) ecosystems are at their northern margin of their range in British Columbia (B.C.). They are among the most unique and threatened in Canada (Erickson 1993, 2000). Native stands have been reduced by urban development and threats such as invasions by alien species. While some Garry oak plant communities in the Pacific Northwest have been described (Riegel and others 1992, Sugihara and others 1987, Thilenius 1968), relationships with environmental factors have not been fully investigated. Further understanding could improve predictive ability and strengthen assessments for conservation and management of the Garry oak habitat.

I studied Garry oak stands on Vancouver Island and the Gulf Islands and developed a plant community classification framework (Erickson 1996). Twenty-six native communities are addressed in this study, including the mosaic of small patch communities and subcommunities. Added to previous, gradient-level work (Erickson 1996, 2000) are individual, community-scale environmental variables.

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[1] An abbreviated version of this paper was presented at the Fifth Symposium on Oak Woodlands: Oaks in California's Changing Landscape, October 22-25, 2001, San Diego, California.

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This research was intended to determine the following:

- Are native plant communities adequately represented and differentiated?
- Is there a strong relationship between communities and particular ecological variables?
- Which are the most important variables to the Garry oak communities?

Methods

Environmental attributes were described along with Garry oak vegetation on 299 plots using standard methodologies (Walmsley and others 1980). The sample covered a wide array of representative sites and geographic areas (Erickson 1996). The database was scaled or transformed as required (e.g., Frank and Lee 1966 for solar values) and a total of 16 environmental variables were developed *(table 1).* The following variables used the inverse: elevation, downed wood cover, *Ah* horizon depth (depth of the organically enriched surface mineral soil), depth to bedrock, Garry oak cover, and Douglas-fir (*Pseudotsuga menziesii*)/Arbutus (*Arbutus menziesii*) cover.

Table 1—*Environmental variables analyzed.*

Abbreviation/ symbol	**Variable name**	**Values**
geog area	Geographic areas	5 Saanich Peninsula, 4 S. Gulf Islands, 3 western shore, 2 Duncan-Nanaimo, 1 N. Gulf Islands
adjinv elev	Adjusted Inverse of Elevation	Values reversed around the mean elevation
solar ind	Solar Index	Frank & Lee (1966) Solar Beam Irradiation Tables for slope and aspect, May 3
topo drain	Topographic drainage	Slope class times surface shape class
m regime	Moisture regime	Numeric values for field assigned classes from wettest (1) to driest (14)
site exp	Site exposure	Sum of numeric values for field notations (wind, saltspray, etc.)
R geol	Bedrock geology	Classes from fine, shale (1) to coarse, granite (7)
site R&r	Site bedrock & rock exposure	Summed cover values for bedrock, shallow humus over bedrock and rock
site min	Site mineral soil exposure	Cover values
soil text	Soil texture	Numeric classes assigned to field textures, from fine to coarse (highest values)
soil cfr	Soil coarse fragments	Percent: field estimates
invDW	Inverse of Downed Wood: cover	Class values
invAh dp	Inverse of Ah horizon depth	Depth in cm.
invRdp	Inverse of depth to Bedrock	Depth in cm.
invQg	Inverse of Garry oak cover	Sum of tree layer cover plus _ the shrub layer cover
invFd&Arb	Inverse of Douglas-fir and arbutus cover	Class values summed

Detrended Correspondence Analysis (DCA) (Hill and Gauch 1980) was undertaken on the variable means for each community within four organizational categories: early-season; bedrock outcrops and rocky; "other native"; and "wet native" *(table 2).*

Table 2—*Native Garry oak plant communities.*

No.	Community name	Ct[1]	T[2]
c37a	*Quercus garryana – Camassia quamash*	E	s
c35a	*Quercus garryana- Camassia quamash- Erythronium oregonum*	E	s
c35b	*Quercus garryana – Camassia quamash – Dodecatheon hendersonii*	E	s
c37b	*Quercus garryana – Camassia quamash – Ranunculus occidentalis*	E	s
c36	*Quercus garryana – Camassia leichtlinii*	E	c
c48	*Quercus garryana – Montia perfoliata*	E	c
c51	*Quercus garryana – Dicranum scoparium – Plectritus congesta*	E	c
c52	*Quercus garryana – Dicranum scoparium*	B	s
c11	*Quercus garryana – Dicranum scoparium – Montia parvifolia*	B	s
c45	*Quercus garryana – Dicranum scoparium – Sedum spathulifolium*	B	s
c46	*Quercus garryana – Rhacomitrium canescens – Selaginella wallacei*	B	c
c26	*Quercus garryana – Mahonia aquifolium*	ON	c
c16a	*Quercus garryana – Lonicera hispidula*	ON	c
c20	*Quercus garryana – Festuca idahoensis*	ON	s
c25	*Quercus garryana – Festuca idahoensis – Cerastium arvense*	ON	s
c27	*Quercus garryana – Festuca idahoensis – Trifolium microcephalum*	ON	s
c42	*Quercus garryana – Festuca idahoensis – Vicia americana*	ON	s
c41	*Quercus garryana – Lathyrus nevadensis*	ON	c
c43	*Quercus garryana – Bromus carinatus*	ON	c
c47	*Quercus garryana – Elymus glaucus*	ON	c
c14	*Quercus garryana – Carex inops*	WN	c
c13	*Quercus garryana – Melica subulata*	WN	c
c15	*Quercus garryana – Holodiscus discolor – Symphoricarpos albus – Polypodium glycyrrhiza*	WN	s
c10	*Quercus garryana – Holodiscus discolor – Symphoricarpos albus – Rhytidiadephus triquetris*	WN	s
c8	*Quercus garryana – Symphoricarpos albus – Rosa nutkana – Lonicera ciliosa*	WN	s
c9	*Quercus garryana – Symphoricarpos albus – Rosa nutkana – Oemleria cerasiformis*	WN	s

[1] Ct (categories): E=early season, B=bedrock outcrops, ON=other native plant communities, WN=wet native plant communities.

[2] T (type): c=communities, s=subcommunities.

DCA is a multivariate method that simultaneously ordinates scores against subjects (in this case environmental data against communities), and vice-versa, using chi-squared distances. Axis (vector) solutions represent the most variation in the dataset. Communities are separated in multivariate space and referenced relative to the de-trended and re-scaled axes. DCA has been used in identifying vegetation/environment relationships for a number of oak woodland settings (Borchert and others 1993, Maranon and others 1999, Nowacki and Abrams 1992).

Output graphs of communities and variables were scaled in common and combined. For graphical interpretation, a proportional circle was positioned to frame each community on axis 1 against 2, then 1 against 3. The adequacy of community differentiation and the strength of an association with a particular variable were judged separately by the extent of conjunction in the community circles *(table 3, fig. 1)*, but across the two axis combinations.

Table 3—*Graphical interpretative classes.*

Community differentiation	
Associated	A conjunction of the variable and the community circle
Distinct	Community circle does not overlap with another community
Strongly differentiated	Community is distinct on both axis combinations
Moderately differentiated	Distinct on one axis combination
Weakly differentiated	Separate from adjacent communities across the two axis combinations, overlaps with each only on one axis.
Environmental Variable associations	
Uniquely associated	Community is solely associated with the same variable on both axis combinations, and vice-versa
Strongly associated	Community is associated with the same variable on both axis combinations, but shares this association with other, overlapping communities
Moderately associated	Community is associated with a variable on one axis combination and obviously influencing its distribution on the second

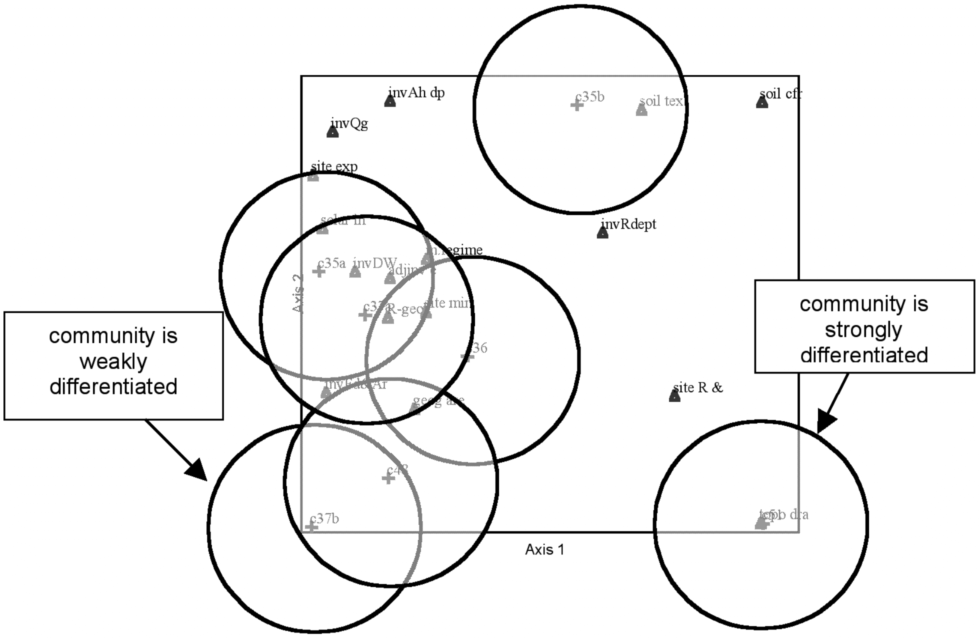

Figure 1 Example of interpretative categories: environmental factors for early season plant communities, axis 1 vs. 2. (Legend for *figures 1-8:* Symbols for each plant community (center of each circle marked with +) are found in *table 1.* Symbols for the environmental variables (scattered throughout the graphs and marked with a triangle) are found in *table 2.*

Results

Plant Community Differentiation

Most of the environmental multivariate space from DCA was covered by communities, when considered across the two axis combinations *(figs. 1-8)*. Three exceptions can be attributed to a lack of intermediate values. In the early season category, Ah horizon depth and soil coarse fragments were not associated with communities on either axis *(figs. 1, 2)*. In the wet native category, considerable space was not covered, but it did not correspond to the location of environmental variables *(figs. 7, 8)*.

Three Garry oak communities were strongly differentiated: *Dicranum scoparium-Plectritus congesta (figs. 1, 2)*; *Carex inops*; and *Holodiscus discolor-Symphoricarpos albus-Polypodium glycyrrhiza (figs. 7, 8)*, of which the first was associated with an environmental variable.

Five other Garry oak communities were moderately differentiated and associated with variables: *Camassia quamash-Dodecatheon hendersonii (figs. 1, 2)*; *Lonicera hispidula*; *Dicranum scoparium-Montia parviflorum (figs. 3, 4)*; *Festuca idahoensis-Trifolium microcephalum*; and *Bromus carinatus (figs. 5, 6)*; the first four of these uniquely so. One community, *Racomitrium canescens-Selaginella wallacei (figs. 3, 4)*, was moderately differentiated but not associated with a particular variable.

Four Garry oak communities: *Camassia quamash-Erythronium oregonum (figs. 1, 2)*; *Dicranum scoparium-Sedum spathulifolium (figs. 3, 4)*; *Festuca idahoensis-Vicia americana (figs. 5, 6)* and *Symphoricarpos albus-Rosa nutkana-Oemleria cerasiformis (figs. 7, 8)* were weakly differentiated, but uniquely associated with variables. Two others: *Lathyrus nevadensis (figs. 5, 6)* and *Holodiscus discolor-Symphoricarpos albus-Rhytidiadelphus triquetris (figs. 7, 8)* were weakly differentiated and not associated with a variable.

Many Garry oak communities (11, or 42 percent) were not differentiated in that they overlapped with adjacent ones on both axis combinations, four of these strongly so. Included were two of the subcommunities which can be identical or have only slight differences in their environmental factors, in that they are separated primarily for their vegetation characteristics. Nevertheless, many (9) of the overlapping communities still had variables associated with them; for most, uniquely so. For example, the *Montia perfoliata (figs. 1, 2)* community was not distinct from adjacent communities, but was associated with the variable, geographic area, on both combinations.

Most (19, or 73 percent) of the communities were also associated with variables on one axis combination. Differentiation for subcommunities (10) exceeded that for communities (5).

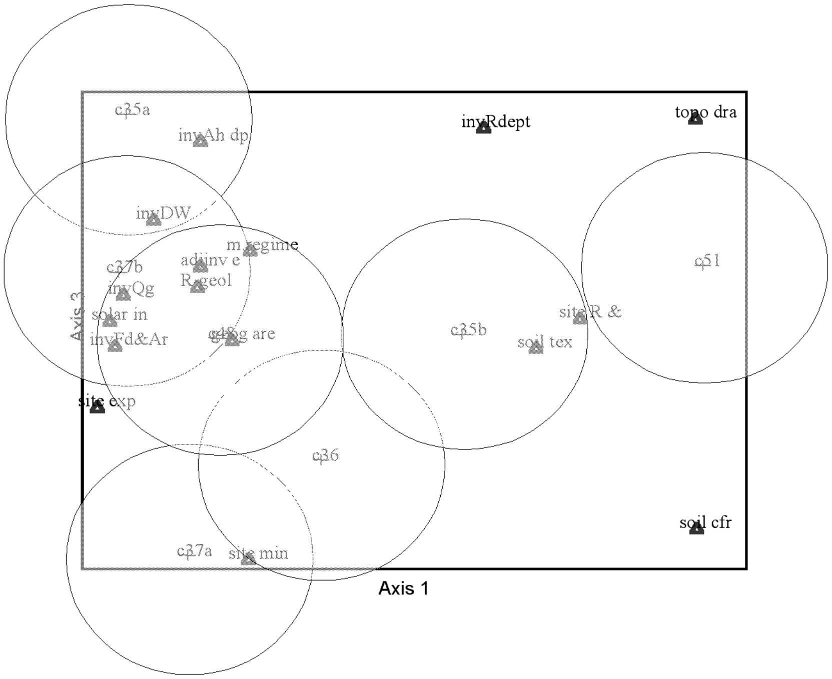

Figure 2 Environmental factors for early season plant communities: axis 1 vs. 3.

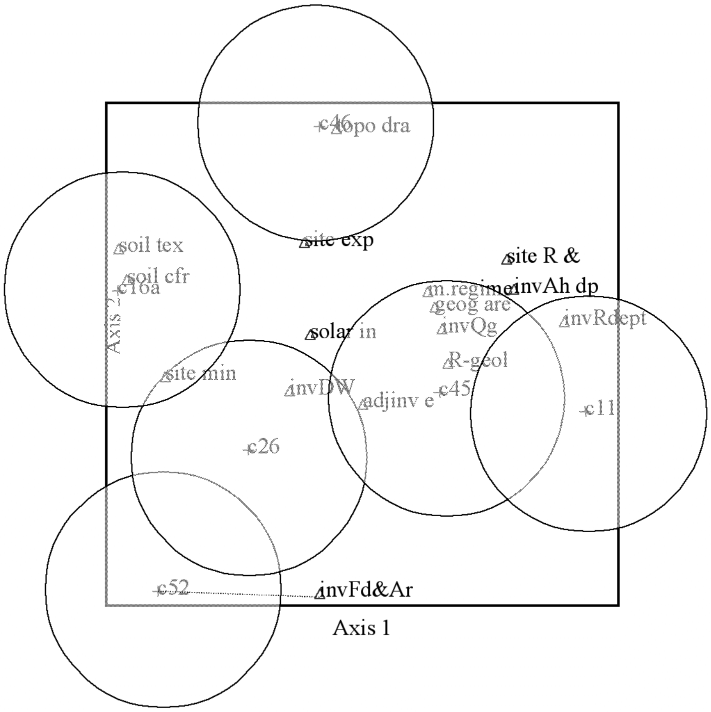

Figure 3 Bedrock outcrop and rocky plant communities and environmental variables: axis 1 vs 2.

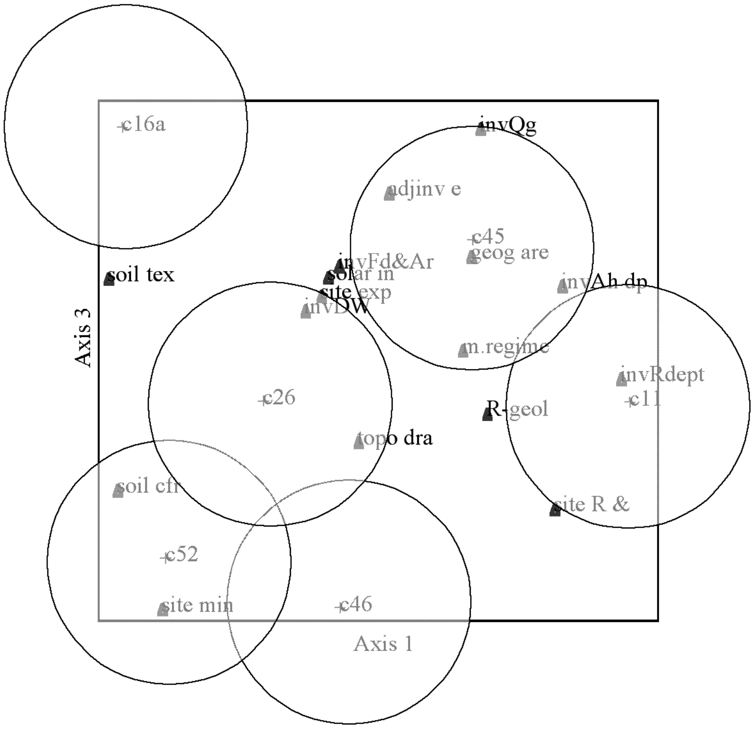

Figure 4 Bedrock outcrop and rocky plant communities and environmental variables: axis 1 vs. 3.

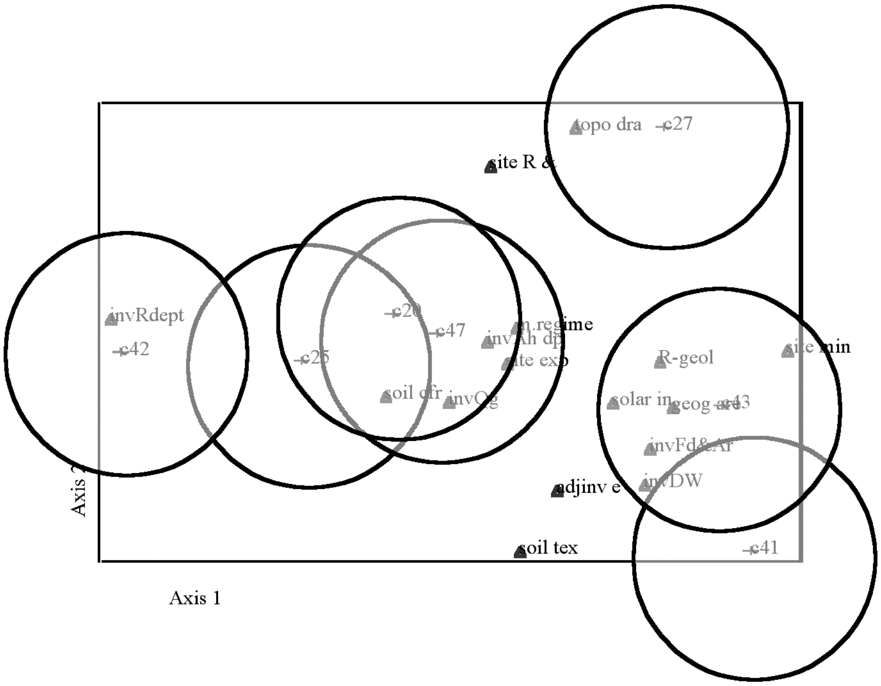

Figure 5 Other native plant communities and environmental variables: axis 1 vs 2.

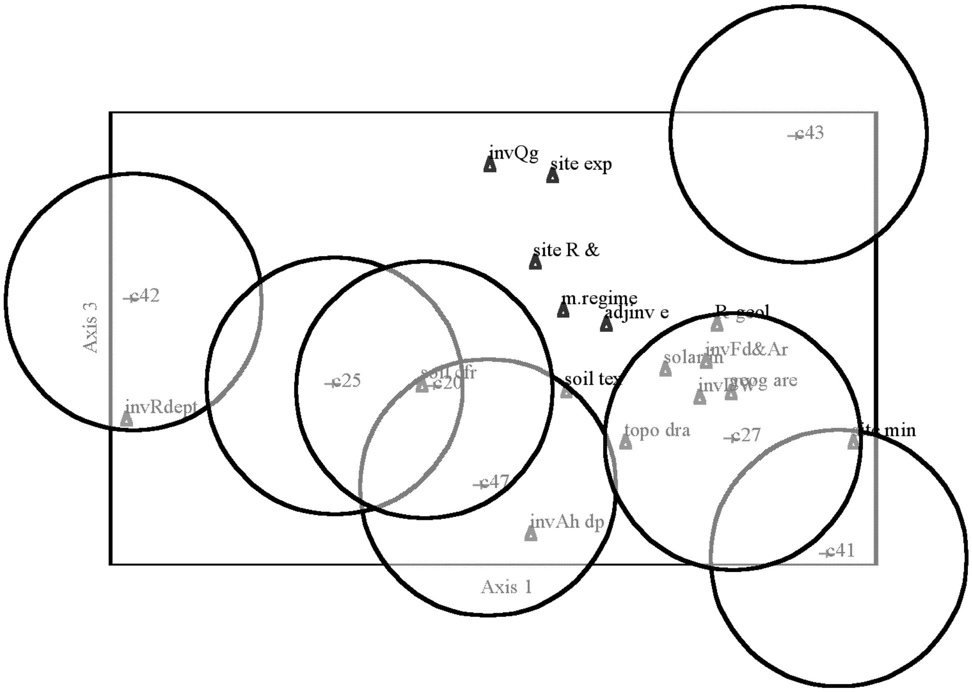

Figure 6 Other native plant communities and environmental variables: axis 1 vs. 3.

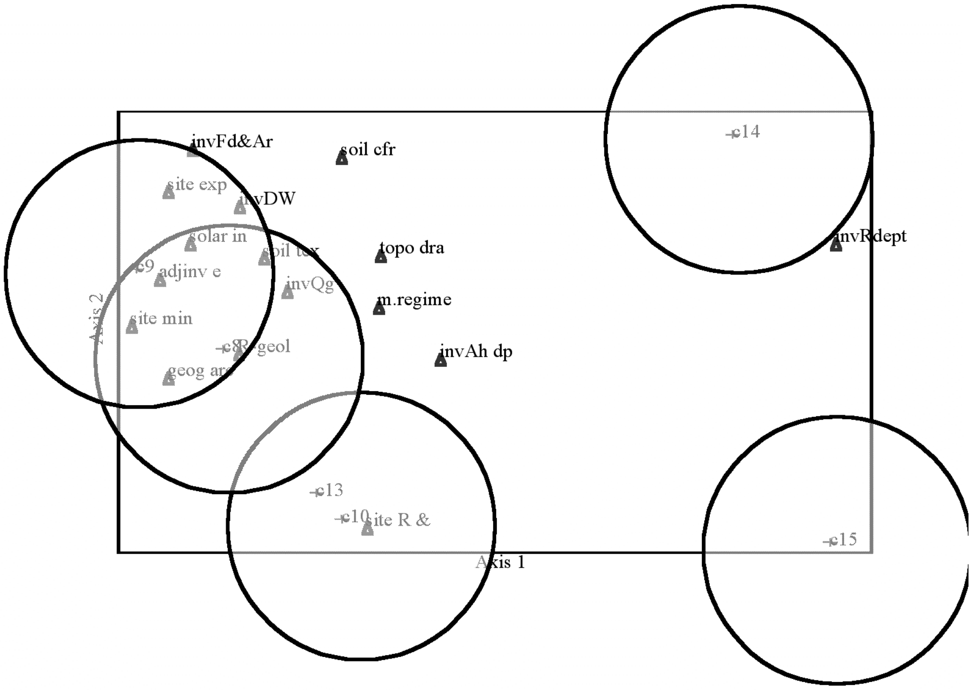

Figure 7 Wet native plant communities and environmental variables: axis 1 vs. 2.

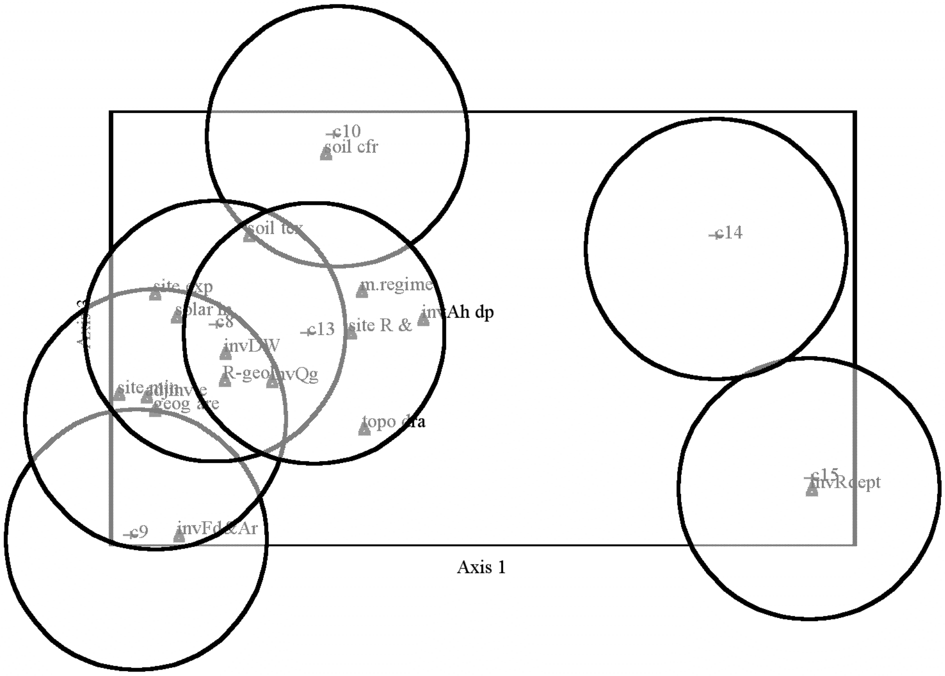

Figure 8 Wet native plant communities and environmental variables: axis 1 vs 3.

Environmental Variables Associated with Individual Communities

Twenty-six associations of environmental variables occurred with particular communities *(figs. 1-8)*, including 13 of the variables. Missing were site exposure, *Ah* horizon depth, and moisture regime. Highest among these, each with five, were associations of site mineral soil exposure, and soil coarse fragments with communities. Geographic area had three associations. A number of variables had two: topographic drainage, soil texture, downed wood, depth to bedrock, elevation, and Garry oak cover.

Site mineral soil exposure was associated with five Garry oak communities (4 unique associations and 1 strong), all with high values: *Camassia quamash* Typic *(figs. 1, 2); Dicranum scoparium* Typic; *Mahonia aquifolium (figs. 3, 4); Bromus carinatus (figs. 5, 6);* and *Symphoricarpos albus-Rosa nutkana-Lonicera ciliosa (figs. 7, 8).*

Soil percent coarse fragments was also associated with five Garry oak communities (3 unique associations and 2 strong): *Dicranum scoparium* Typic; *Lonicera hispidula (figs. 3, 4); Festuca idahoensis*; and *Festuca idahoensis-Cerastium arvense (figs. 5, 6):* each with high values in the data; and *Elymus glaucus (figs. 5, 6),* with moderate values.

Geographic area was strongly associated with three Garry oak communities: *Dicranum scoparium-Sedum spathulifolium (figs. 3, 4)* and *Montia perfoliata (figs. 1, 2),* with high values; and *Symphoricarpos albus-Rosa nutkana-Lonicera ciliosa (figs. 7, 8),* with moderate values in the data. High values indicate a more south-easterly (warmer, drier) distribution; moderate values a more mixed distribution; and for both: probably also biogeographic differences associated with a history on the main island.

Topographic drainage was strongly or moderately associated with two Garry oak communities: *Dicranum scoparium-Plectritus congesta (figs. 1, 2)* (on convex sites which rapidly shed soil moisture); and *Festuca idahoensis-Trifolium microcephalum (figs. 5, 6),* both of which had high values.

Soil texture was strongly associated with two Garry oak communities: *Camassia quamash-Dodecatheon hendersonii (figs. 1, 2),* and *Lonicera hispidula (figs. 3, 4),* both of which had high values (coarse soils).

Depth to bedrock was strongly associated with two Garry oak communities: *Dicranum scoparium-Montia parviflorum (figs. 3, 4)* and *Festuca idahoensis-Vicia americana (figs. 5, 6),* both with high values for their shallow soils relative to others within their category.

Downed wood was strongly or moderately associated with two Garry oak communities: *Camassia quamash-Erythronium oregonum (figs. 1, 2)* and *Mahonia aquifolium (figs. 3, 4),* both of which had low cover in their community means.

Elevation was uniquely or strongly associated with two Garry oak communities: *Symphoricarpos albus-Rosa nutkana-Lonicera ciliosa (figs. 7, 8)* and *Dicranum scoparium-Sedum spathulifolium (figs. 3, 4),* both of which had low elevations. The same two communities also had a relationship with Garry oak cover (high covers on the former, low on the latter).

Douglas-fir and Arbutus cover was strongly associated with one Garry oak community, *Symphoricarpos albus-Rosa nutkana-Oemleria cerasiformis*, with a relative deficiency of cover for these trees. These sites are multi-layered, deciduous shrub thickets.

Site bedrock and rock exposure was strongly associated with one Garry oak community: *Melica subulata (figs. 7, 8),* which had moderately high values.

The remaining variables in this set, bedrock geology and solar insolation, were strongly associated with one Garry oak community, *Symphoricarpos albus-Rosa nutkana-Lonicera ciliosa (figs. 7, 8),* which also had one variable (geographic area) above. Their high values suggest sites with coarse, nutrient poor bedrock on steep south and southwesterly-facing slopes, relative to others within the “wet” category.

All 16 variables were found in conjunction with communities on one axis combination, except depth to bedrock (which had several strong associations).

Discussion

The results indicate an adequate degree of differentiation in the community framework. Fifteen communities were distinct in the interpretive graphing. Of those not differentiated, two were subcommunities not expected to differ in their environmental relationships, six were uniquely associated with environmental variables, leaving three communities not accounted for. However, communities may not correspond to extreme values of any particular variable, especially if they have intermediate moisture relations. The Garry oak-*Elymus glaucus* community, for example, was found with moderate values of soil coarse fragments; low values for moisture regime, site exposure and Garry oak cover; and moderate values for soil texture; the latter four variables all on one axis combination.

Differentiation for subcommunities (10) exceeded that for communities (5), suggesting that subcommunities may not be sharing the same ecological sites. Short temporal-scale, within-community plant succession may characterize recovery after minor disturbance in these subcommunities. For example, in Garry oak habitat, *Festuca idahoensis-Trifolium microcephalum* may lead to *Festuca idahoensis-Cerastium arvense* and then to a *Festuca idahoensis* subcommunity (Erickson 1996). There could be corresponding site-level environmental changes, such as decreasing bare mineral soil exposure. The results on differentiation could be used to modify the concepts or placement of subcommunities. Either site differences and moderate vegetation differences could be recognized, or the more distinct subcommunities could be elevated to communities. The differentiation results on their own do not compellingly suggest classification changes, but they could contribute to a review which includes vegetation comparisons.

The environmental variables were adequately represented by the community framework, with most of the environmental multivariate space covered by communities. In the early season category, *Ah* horizon depth and soil coarse fragments were not covered, suggesting potential additions of communities with intermediate values for these variables. In the wet native category, considerable space was not covered, but it did not correspond to the location of environmental variables. Instead, these gaps seem to result from the fact that the values for depth to bedrock were strongly skewed in both directions. Compensating factors, such as the inflow of soil moisture from bedrock, might also mask a vegetation response to intermediate values.

The strength of the associations for these variables does not present evidence for a 1:1 relationship between sites and communities. Environmentally-distinct communities with single identified variables comprise about 58 percent of the total. Plant communities have been taken as the integrators of site conditions. However, with subtle site differences and variations in biogeographic and disturbance histories, it is unlikely there will ever be total predictability. Many communities may respond to a suite of environmental variables, rather than to one outstanding variable.

Soil coarse fragments, site mineral soil exposure, and geographic area were the most important variables in the community framework, followed by topographic drainage, soil texture, depth to bedrock, percent downed wood, and elevation. The remaining variables were associated with only one or with no communities. These results differ from previous gradient-level multiple regression work (Erickson 1996, 2000), but this is attributed to the difference in scale. The present work addresses small-patch communities scattered in a mosaic, as may be appropriate for discontinuous distributions at a range margin.

Applying the environmental relationships from this study could advance both site and vegetation assessments in preservation initiatives, and predictive ability for restoration work in Garry oak habitat. With the addition of numeric thresholds, an environmental key could be developed which would allow ecological sites to be assigned to plant communities in the absence of vegetation information. These relationships could be applied in broad ecological surveys, such as predictive mapping. A tested, refined, and more ecosystematic plant community classification should stimulate wider application and therefore encourage the conservation of these important elements of biodiversity.

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Arboreal Seed Removal and Insect Damage in Three California Oaks[1]

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Abstract

We investigated arboreal removal and insect damage to acorns in an undisturbed oak woodland in central coastal California. Arboreal seed removal was determined for four to eight individual *Quercus lobata* trees over a period of 14 years by comparing visual estimates of the acorn crop with the number of acorns caught in seed traps. Insect damage was assessed by sampling acorns from trees of all three species of oaks common in the study site (*Quercus lobata, Q. douglasii,* and *Q. agrifolia*). Patterns were generally similar for both sets of data: more acorns, but a smaller proportion of the crop, were removed or damaged as the productivity of an individual tree increased. However, we found no evidence that trees outproducing local conspecifics attracted a disproportionate number of arboreal seed or insect predators. Acorn removal was not significantly correlated with population sizes of either California scrub-jays (*Aphelocoma coerulescens*) or acorn woodpeckers (*Melanerpes formicivorus*), two common arboreal seed removers that are also potentially important dispersal agents. These patterns are partially in accord with predator satiation, but not the attraction of seed dispersers, being an important factor potentially influencing the reproductive strategies of oaks in central coastal California.

Introduction

Patterns of seed production, including reproductive synchrony on a geographically large scale or masting (Kelly and Sork [In press]), Silvertown 1980), may be explained by two general hypotheses. First is resource matching, which proposes that masting is associated with years in which resources are more available, and second are economies of scale, which propose that synchrony arises from the potential energetic advantages to individuals within a population of investing more into reproduction synchronously every few years rather than less each year, given an overall constraint to the total level of reproductive effort (Norton and Kelly 1988).

Economies of scale include energetic advantages related to wind pollination (Norton and Kelly 1988, Smith and others 1990), predator satiation (Ims 1990a, 1990b; Janzen 1971), and the attraction of seed dispersers (Givnish 1980, Sork and others 1983). As traditionally envisioned, the importance of predator satiation is

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dependent on the ability of highly productive trees to overwhelm seed predators, thereby resulting in a negative correlation between the size of the seed crop and the proportion of seeds depredated (Norton and Kelly 1988). Selection for reproductive synchrony should be particularly intense depending on neighborhood effects, that is, the crop of a particular tree relative to the area as a whole (Sargent 1990). Trees outproducing the local area should suffer increased seed predation and there will be selection to synchronize reproductive effort within the population.

Alternatively, if the attraction of seed dispersers is important, trees should produce fruit in ways which differentially attract potential seed dispersers and lead to a relatively high proportion of seeds removed being cached rather than eaten. Thus, the optimal pattern of seed production for an individual tree depends on the potentially complex and generally unknown relationship between the proportion of seeds cached by animals, the efficiency with which cached seeds are recovered, the reproductive effort of an individual tree, and overall seed availability in a particular year. If neighborhood effects are strong, some trees should invest heavily in reproduction each year in order to outcompete other conspecifics and ensure the attraction of potential dispersal agents. On the other hand, an individual tree producing a large crop in a year when all other trees fail will presumably suffer heavy predation as animals attracted to the tree eat rather than cache most of the acorns they remove.

The expected result of these conflicting selection pressures is not likely to be straightforward (Ims 1990a). Presumably these competing considerations are likely to result in moderate to low reproductive synchrony (Koenig and others 1994a). With respect to the size of the acorn crop per se, we can expect a positive correlation between a tree's seed crop and not only the number but also the proportion of acorns removed if productive trees successfully attract proportionately more dispersers than unproductive trees.

A third possibility is that primary seed predators are generalists switching from alternative food resources, in which case Ims (1990a, 1990b) has shown that the expected pattern of reproduction is one of asynchrony rather than synchrony. Given the vast array of both vertebrate and invertebrate acorn predators, it is thus not possible to confidently predict the optimal pattern of reproduction in response to predation in this system (Koenig and others 1994a). Consequently, we restrict ourselves to the more traditional form of predator satiation discussed above.

Invertebrate users of oaks (genus *Quercus*, family Fagaceae) are particularly extensive: as many as 5,000 insect species are associated with oaks in California, of which approximately 800 use some portion for food (Pavlik and others 1991). In addition, over 170 species of birds and mammals are dependent on oak habitats in California and nearly 100 species are known to feed on acorns in the United States, making *Quercus* one of the most important genera of woody plants to wildlife in North America (Barrett 1980, Christisen and Korschgen 1955, Martin and others 1951, Van Dersal 1940, Verner 1980). Given this impressive assemblage of animals, it is likely that predation is important to reproductive patterns of oaks. In return, oaks disperse their seeds largely by taking advantage of animals that fail to remove some proportion of acorns that they have moved and cached (Smith and Folmer 1972, Sork and others 1983). Particularly significant in this respect are jays (family Corvidae); birds of this family are common seed removers (Darley-Hill and Johnson 1981) and, since they store acorns in the ground, are excellent dispersal agents (Carmen [In press], Grinnell 1936, Vander Wall 1990).

This paper is one of a series devoted to understanding acorn production patterns of California oaks. Here we discuss the factors influencing arboreal acorn removal, primarily by birds, and predation on acorns, again prior to acorn fall, by insects; we do not discuss seed predation on sound acorns after they have fallen from the tree. We focus on three questions. First, what is the intensity of arboreal acorn removal and and of insect predation? Second, what factors influence the extent of these phenomena? Third, does the pattern of acorn removal and insect damage suggest an important role for either predator satiation or the attraction of seed dispersers in the evolution of oak reproductive patterns?

Methods

The study was conducted at Hastings Reservation, a 900-ha reserve located in the Santa Lucia Mountains of central coastal California, approximately 42 km inland from Monterey. Elevation at the study site ranges from 460 to 950 m. This area experiences a Mediterranean climate in which virtually no rain falls during the summer and early fall (June-September). Annual rainfall ranges from 26.1 to 111.2 cm, with a 50-yr mean of 55 cm. In all areas of the study site oak (*Quercus*) is the dominant genus of tree. Five species are common, but only three are widespread throughout the site: *Quercus lobata* (valley oak), *Q. douglasii* (blue oak), and *Q. agrifolia* (coast live oak). These are joined locally, mostly at higher elevations, by *Q. chrysolepis* (canyon live oak) and *Q. kelloggii* (California black oak).

Arboreal Seed Removal

Eight large, mature *Quercus lobata* trees were used. Four, sampled from 1980-1989 and 1992-1996, were located on level ground in the floodplain about 0.5 km from the reserve headquarters, while the other four, sampled from 1992-1996 only, were located in an old field on a hill 0.75 km from headquarters.

For each tree, we estimated the extent of arboreal seed removal by comparing visual estimates of the acorn crop made prior to acorn fall with the number of acorns collected from seed traps. Visual estimates involved having two experienced observers scan different areas of each tree's canopy and count as many apparently viable acorns as possible in 15 seconds. Counts were made each autumn in September or early October at the height of the acorn crop prior to acorn fall. The total number of acorns counted by both observers was added to yield acorns counted per 30 seconds and then log-transformed to reduce the correlation between the mean and variance (Sokal and Rolf 1969). For further details on this survey method, see Koenig and others (1994b). Log-transformed values for the four (or eight) trees were averaged to estimate the mean crop of the focal trees for each year.

Acorn fall under each of the focal trees was sampled using seed traps consisting of plastic garbage bags held in place by hogwire frames. Each trap was approximately 0.25 m^{-2} in area and permanently located around the tree about half-way between the trunk to the edge of the tree's canopy. Each trap was assumed to sample an approximately equal volume of canopy. Four traps per tree were used. Traps were checked at weekly intervals throughout the period of acorn fall and the total number of acorns caught summed for all traps for a given tree throughout the season.

Arboreal seed removal was estimated as follows. First, we plotted the relationship between the two measures of the acorn crop for the individual trees (figure 1). The expected number of acorns trapped was estimated from a line drawn from the origin to the point yielding a line of maximum slope (point A); the formula for this line is $y = 1.259\ x$, where y is the number of acorns trapped and x is the number of acorns counted (both log-transformed). This conservatively assumes that point A represents no seed removal and, given this assumption, the deviation of the other points from the line provides an estimate of the extent of arboreal seed removal. Values for the expected and observed numbers of acorns trapped were then back-transformed (to acorns m^{-2}), from which we estimated both the total number of acorns (per trap) that were apparently removed by arboreal seed predators (the "total" number of acorns removed) and the proportion of acorns produced that were removed by arboreal seed predators (the "relative proportion" of acorns removed). Values were then averaged within years to derive mean annual values. Trees and years in which no acorns were produced were excluded, since the number and proportion of acorns removed in such cases were indeterminate. This left samples for 61 trees over a period of 14 years (none of the trees sampled produced any acorns in 1983).

In addition to the focal trees, an additional 37 *Q. lobata* trees within 1 km of the focal trees were visually sampled at Hastings each autumn in order to assess the overall acorn crop. The average number of (log-transformed) acorns counted in these trees was used as a measure of the overall acorn crop. Results were not substantively changed if all sampled trees (including 25 *Q. douglasii* and 27 *Q. agrifolia*) within 1 km were used instead. Neighborhood effects, that is, the effect of local seed density on removal from individual trees (Sargent 1990) were investigated by comparing the estimated proportion of acorns removed from trees that outproduced an average tree in the full *Q. lobata* sample with those that produced fewer acorns than the full sample, based on the number of acorns counted per 30 seconds.

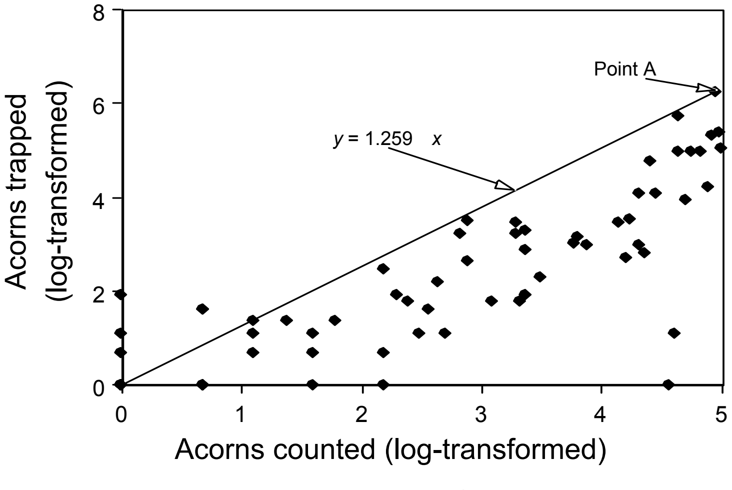

Figure 1—Relationship between the number of acorns counted by visual censusing per tree and the number caught in four 0.25-m^2 acorn traps; both variables are log transformed. Four *Quercus lobata* trees were measured for each of 10 years (1980-1989) and the same four plus four additional trees were measured for an additional four years (1992-1995); each point represents an individual tree. The formula is for the line drawn from the origin to point A, the point highest in the quadrant and therefore yielding the greatest slope. This assumes a linear expected relationship between the variables and no seed removal between the acorn census and acorn fall for point A.

Population densities of acorn woodpeckers (*Melanerpes formicivorus*) and California scrub-jays (*Aphelocoma californica*), two of the major arboreal seed predators on the study site, were estimated based on concurrent long-term studies of marked individuals of these species (Koenig and Mumme 1987, Carmen in press). Densities of acorn woodpeckers were known for all 15 years of the study, while those for California scrub-jays were known from 1981 to 1986. For the latter species, the number of residents, plus the estimated number of floaters present in the fall, were added together. Densities used were the number of individuals present within 1 km of the focal trees during October.

Insect Predation

Each year between 1984 and 1995 we collected 20 to 25 acorns from as many trees as possible during the acorn survey in the autumn. Acorns were dried at room temperature and later shelled, at which time insect damage was assessed and the relative proportion of acorns suffering damage determined. This proportion was multiplied times the number of acorns counted to yield an index of the total number of acorns damaged by insects in the tree. These values were correlated with the acorn production of individual trees and the mean overall acorn crop of trees for each species for each year. We included only the three most widespread species (*Q. lobata, Q. douglasii*, and *Q. agrifolia*) for which we had the largest sample sizes.

Neighborhood effects were investigated by calculating the correlation between the amount of insect damage for each sampled tree and the difference between its acorn crop and the mean crop of other conspecifics surveyed within 100 m, 250 m, and 1 km that year.

Two-tailed probability values for statistical tests are reported when possible; *P*-values < 0.05 are considered significant.

Results

Arboreal Seed Removal

There was a significant correlation between the acorn crop as determined from the visual survey and from the seed traps of the four (or eight) focal *Q. lobata* trees ($r_s = 0.86$; $N = 72$, $P < 0.001$; *fig. 1).* At very low crop sizes, acorns were sometimes caught in the traps even though none was counted. At larger crop sizes, arboreal seed removal usually resulted in fewer acorns being trapped than expected from the visual counts. In one case, no acorns were trapped even though 96 were counted in the 30 second visual survey.

We calculated both the total number and relative proportion of acorns removed prior to seed fall each year *(table 1).* These values were not significantly correlated using either the mean annual ($r_s = -0.23$, $N = 14$ years, $P = 0.42$) or individual tree data ($r_s = 0.19$, $N = 57$ trees, $P = 0.16$).

Correlations of the measures of arboreal seed removal with variables related to the acorn crop and the population sizes of the two avian acorn specialists are given in table 2. In general, as acorn productivity of either the focal trees or the overall area increases, the total number of acorns removed increases, while the relative proportion of acorns removed decreases, albeit only slightly *(fig. 2).* Relationships with the population sizes of both acorn woodpeckers and California scrub-jays were in the same direction. That is, when population size of either of these species was greater, they were apparently able to harvest more acorns but a smaller proportion of the overall crop from the focal trees. However, these correlations were not significant.

Table 1—*Acorn production and population size of potential predators. Acorn production values are means of log-transformed number of acorns counted per 30 seconds for the four (1980-1989) or eight (1992-1995) focal* Q. lobata *trees. Overall mean acorn crop values average counts for 34* Q. lobata *trees sampled within 1 km (but excluding) of the focal trees.*

Year	Overall mean acorn crop	Focal tree: Acorns counted	Focal tree: Number removed (m^{-2})	Focal tree: Pct removed	Population size: Acorn woodpeckers	Population size: California scrub-jays
1980	0.92	1.68	20.8	83.8	43	
1981	1.79	2.24	183.9	66.0	41	97
1982	1.54	2.86	62.4	93.5	43	74
1983	0.22	0.00	—	—	8	14
1984	0.71	0.17	1.4	100.0	41	29
1985	4.01	3.70	226.3	38.5	66	40
1986	1.25	0.40	6.6	100.0	49	47
1987	3.58	4.13	143.1	61.3	61	—
1988	2.09	0.62	1.4	34.8	74	—
1989	1.83	3.62	176.2	99.0	64	—
1992	3.02	3.42	120.4	56.1	46	—
1993	1.20	1.69	9.8	48.0	63	—
1994	2.56	3.68	150.9	82.8	83	—
1995	0.46	0.37	2.8	98.2	47	—
1996	2.07	3.20	77.0	57.8	41	—

We looked for a neighborhood effect by comparing the estimated proportion of the acorn crop removed for trees that outproduced the overall mean acorn crop (N = 44) with those producing fewer acorns than the mean overall acorn crop (N = 13), excluding trees for which we counted no acorns (N = 15). There was no significant difference between these two categories of trees (Mann-Whitney U-test, z = 0.9, P = 0.35). As an additional test, we restricted analysis to within years and compared the proportion of acorns removed from the tree producing the largest crop with the one producing the smallest (non-zero) crop. In only seven out of 12 (58 percent) years with two trees producing different-sized crops, the tree with the smaller crop had the higher proportion of acorns removed. Thus, neither test provides strong evidence that a larger proportion of the acorn crop is removed arboreally by animals when a tree produces more acorns than the average tree in the study area.

Table 2—*Spearman rank correlations between annual mean values of variables potentially related to the extent of arboreal seed removal. Overall mean acorn crop values as in Table 1.* * P *<0 .05,* *** P *<0.001 (two-tailed); other* P *>0.05.*

	Pct acorns removed	Total number of acorns removed	*N* years
Mean crop of focal trees	-0.41	0.85***	14
Overall mean acorn crop	-0.62*	0.65*	14
Acorn woodpecker population size	-0.34	0.16	14
California scrub-jay population size	-0.31	0.40	5

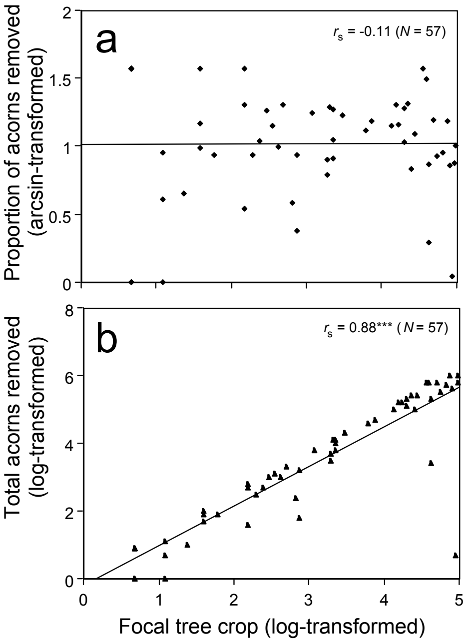

Figure 2—Relationships between relative (a) and total (b) extent of acorns removed arboreally from four (eight in four years) *Quercus lobata* trees measured over 14 years and the acorn crop of the focal tree based on visual censuses. Trees failing to produce any acorns are excluded. Values are estimated from the difference between the observed and expected acorns captured in traps given the number counted visually.

Insect Predation

Correlations were significantly positive between the relative proportion and total amount of insect damage to acorns (r_s= 0.43 [*N* = 157 trees], 0.36 [*N* = 141], and 0.82 [*N* = 131] for *Q. lobata*, *Q. douglasii*, and *Q. agrifolia*, respectively; all *P* < 0.001). With the exception of a slight increase in the proportion of *Q. agrifolia* acorns damaged as productivity increased, the proportion of acorns damaged decreased and the total number of acorns damaged increased with focal tree productivity (figure 3). This pattern was also evident in an ANCOVA combining all trees and years (table 3). Using annual means, correlations were mostly nonsignificant, but the trends were the same, and larger acorn crops correlated with significantly higher total insect damage in *Q. agrifolia (table 4).*

Table 3—*Analysis of covariance of relative proportion and total insect damage to acorns for three species of California oaks. Analyses first control for the main factors and then for the covariate. Presented are the partial* F*-values for the variables and whether they are significant. For the covariate, the direction of the regression line (positive or negative) is in parentheses. Degrees of freedom are (. , 397), where the numerator is the number in parentheses after the variable.* * P *<0.05,* *** P *<0.001.*

		Pct insect damage	Total insect damage
Main factors	Species (2)	1.6	1.3
	Year (10)	7.8***	14.8***
Interaction	Species x year (18)	1.7*	1.7*
Covariate	Focal tree crop (1)	2.6 (-)	276.5*** (+)
Explained (31)		4.8***	16.5***

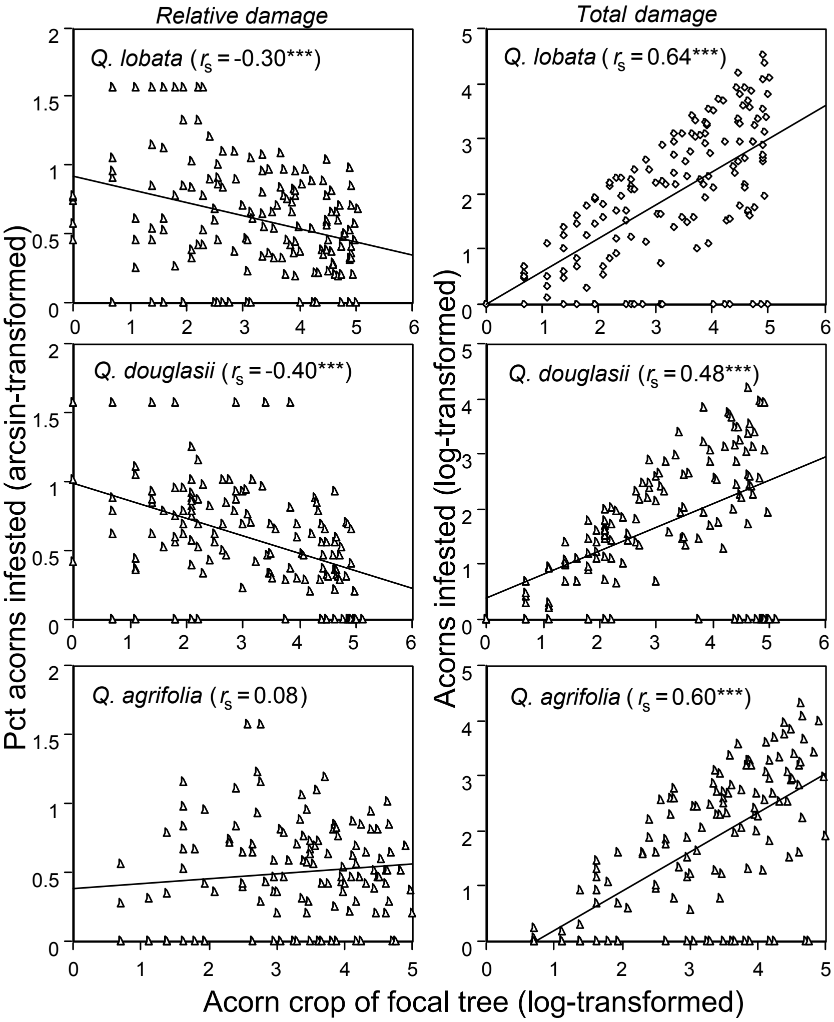

Figure 3—Relationships between relative (left side) and total (right side) extent of insect damage to acorns from three species of oaks and the acorn crop of the focal tree based on visual censuses.

Neighborhood effects were investigated by examining the degree of insect damage vis-à-vis the degree to which focal trees outproduced or underproduced acorns compared to nearby conspecifics. In general, correlations were not significant, with the exceptions of *Q. lobata* and *Q. douglasii* compared to conspecifics within 1 km *(table 5)*. In both these cases, trees that outproduced conspecifics tended to suffer less relative insect predation than trees underproducing conspecifics.

Table 4—*Spearman rank correlations between the mean overall acorn productivity of three species of oaks and the mean relative and total extent of insect damage. Samples sizes are years.* * P *<0.05 (two-tailed); other* P *>0.05.*

	Mean pct acorns damaged	**Mean total number of acorns damaged**	***N* years**
Quercus lobata	-0.26	0.35	11
Quercus douglasii	-0.55	0.35	10
Quercus agrifolia	0.36	0.73*	10

Table 5—*Spearman rank correlations (N trees) between the proportion of insect damaged acorns and the difference between the acorn crop of the focal tree and the mean acorn crops of conspecific trees within 100 m, 250 m, and 1 km. Positive correlations indicate that trees with relatively large acorn crops suffer relatively greater insect damage, whereas negative correlations indicate the converse.* * P *<0.05; other* P *>0.05.*

	Comparison population: conspecifics within		
	100 m	**250 m**	**1 km**
Quercus lobata	-0.09 (147)	-0.06 (157)	-0.19* (157)
Quercus douglasii	-0.13 (125)	-0.13 (141)	-0.21* (141)
Quercus agrifolia	0.13 (104)	0.02 (131)	-0.10 (131)

Discussion

Implications for Masting

A primary prediction of the predator satiation hypothesis as traditionally viewed is that there should be an inverse correlation between productivity and the proportion of seeds depredated. This prediction was upheld in two of the three species for insect damage *(fig. 3)* and was also true, albeit only weakly, for arboreal seed removal *(fig. 2)*. In all cases, the total number of acorns damaged or removed increased with larger seed crops. In the case of insect predation, this was true to some extent even after controlling for year and species differences *(table 3).* This suggests that seed predators may be an important influence synchronizing acorn production among California oaks.

Crop size of an individual tree is not the only factor potentially influencing the extent of acorn removal: local seed density may be important as well. Such neighborhood effects were not detected for arboreal seed removal, which was apparently independent of the size of the overall acorn crop. Evidence for neighborhood effects was also weak with respect to insect damage, where the only significant results indicated that trees producing more acorns than local conspecifics suffered relatively less insect damage than trees producing fewer acorns *(table 5).* These results are in the opposite direction from those predicted by the hypothesis that synchrony is reinforced by the inordinate attractiveness of trees outproducing neighbors. Instead, trees with larger acorn crops than local conspecifics suffer relatively less, rather than more, insect damage.

What is the selective effect of these patterns on the reproductive effort of oaks at Hastings Reservation? To the extent that the proportion of acorns removed and the incidence of insect damage decreases as the acorn crop of a tree increases, it suggests that predator satiation occurs at both these levels. These relationships should select for masting, at least once year-to-year variation in weather-mediated resource availability initiates some degree of synchronization in acorn crop size (Lalonde and Roitberg 1992). However, we found no detectable disadvantage to individual trees that outproduced conspecifics in terms of either increased arboreal seed removal or increased incidence of insect damage to their acorns. Thus, the synchronizing effects of these phenomena at the neighborhood level do not appear to be strong.

Which is more important to the masting patterns of oaks: arboreal seed removal or insect predation? The estimated percent of acorns removed prior to acorn fall ranged between 34.8 and 100 percent *(table 1),* whereas the mean annual proportion of acorns infested with insects varied from 0 to 63 percent, suggesting that arboreal seed removal may be greater. However, these figures may be misleading for at least two reasons. First, insect damage could only be assessed in trees with relatively large acorn crops, since adequate samples could not be obtained from trees with small crops. Because the proportion of acorns damaged decreases with crop size *(fig. 2),* our samples are biased toward trees that are likely to have relatively low insect predation. Second, arboreal seed removers, in contrast to insects, are both predators and important dispersal agents. California scrub-jays, for example, store acorns extensively in the ground where many may eventually sprout (Carmen [In press], Grinnell 1936), and even acorn woodpeckers, which store acorns in granaries from which relatively few acorns eventually escape destruction (Koenig and Mumme 1987), inadvertently drop some acorns in while caching them. Consequently, it is likely that trees may ultimately benefit by attracting individuals of these two species, despite the fact that many of the acorns they remove are destroyed rather than dispersed. Fruiting strategies of individual oaks should be designed to reduce the extent of insect damage to acorns, but may benefit by attracting, rather than evading, arboreal seed removers, at least when conditions are such that some of the seeds removed are cached rather than eaten immediately.

Although acorn dispersal by arboreal seed removers such as scrub-jays is certainly important to the long-term survival of oaks, to what extent does the attraction of such dispersal agents appear to have influenced masting strategies? Two predictions can be made by this hypothesis: (1) in years when population sizes of arboreal seed removers are greater, more acorns, both proportionately and in total, should be dispersed, and (2) there should be a significant neighborhood effect in that trees outproducing the overall mean acorn crop should attract relatively many arboreal seed removers, potentially leading to a higher proportion of acorns dispersed. Our data are not definitive since we examined only acorn removal and not the probability of dispersal per se. However, to the extent that arboreal acorn removal is an index of caching, neither of these predictions was upheld. First, the correlation between population sizes of California scrub-jays and acorn woodpeckers, two major seed removers, and both the relative and total number of acorns removed were not significant *(table 2),* and second, no significant neighborhood effect was found with respect to arboreal acorn removal. These results fail to support the hypothesis that the attraction of seed dispersers is a major influence on seed production patterns in this population.

In contrast, the observed patterns of reproduction are generally consistent with both predator satiation as traditionally envisioned or an alternative hypothesis, that of increased pollination efficiency due to wind pollination, being important factors leading to masting. Both these hypotheses successfully predict relatively low variation in acorn production within years, high variation in acorn production among years, and the existence of crop failures (Koenig and others 1994). Thus, the satiation of predators, both arboreal and insect, may be an important factor tending to synchronize reproduction by oaks in central coastal California. Acorn dispersal by arboreal seed removers does not appear to be the dominant factor influencing the reproductive strategies of oaks in our population, although it may still be a factor countering the within-population synchrony observed in the population.

Acknowledgments

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Insect-oak Interactions with Coast Live Oak (*Quercus agrifolia*) and Engelmann Oak (*Q. engelmannii*) at the Acorn and Seedling Stage[1]

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Abstract

We determined the impact of insects on both acorns and seedlings of coast live oak (*Quercus agrifolia* Nee) and Engelmann oak (*Quercus engelmannii* E. Greene). Our goals were to (1) identify insects feeding on acorns and levels of insect damage, and (2) measure performance and preference of a generalist leaf-feeding insect herbivore, the migratory grasshopper (*Melanoplus sanguinipes* [Fabricus] Orthoptera: Acrididae), on both species of oak seedlings. Acorn collections and insect emergence traps under mature *Q. agrifolia* and *Q. engelmannii* revealed that 62 percent of all ground-collected acorns had some level of insect damage, with *Q. engelmannii* receiving significantly more damage. However, the amount of insect damage to individual acorns of both species was slight (<20 percent damage per acorn). *Curculio* occidentis (Casey) (Coleoptera: Curculionidae), *Cydia latiferreana* (Walsingham) (Lepidoptera: Tortricidae), and *Valentinia glandulella* Riley (Lepidoptera: Blastobasidae) were found feeding on both species of acorns. No-choice and choice seedling feeding trials were performed to determine grasshopper performance on the two species of oak seedlings. *Quercus agrifolia* seedlings and leaves received more damage than those of *Q. engelmannii* and provided a better diet, resulting in higher grasshopper biomass.

Introduction

The amount of oak habitat in many regions of North America is decreasing due to increased urban and agricultural development (Pavlik and others 1991). In addition, some oak species are exhibiting low natural regeneration. Although the status of Engelmann oak (*Quercus engelmannii* E. Greene) natural regeneration has been confirmed in several studies (Muick and Bartolome 1986, Osborne 1989), the increased urbanization in these areas is cause for additional research that seeks to provide management methods to ensure the maintenance of Engelmann oak stands. Engelmann oak is a species of concern in California due its limited distribution and occurrence in the growing urban areas surrounding Los Angeles and San Diego (Osborne 1989). Another oak species co-occurring with *Q. engelmannii* throughout most of its range, coast live oak (*Quercus agrifolia* Nee), also has exhibited reduced

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natural regeneration in central California (Muick and Bartolome 1986). A lack of natural regeneration of this oak has not been identified for southern California; however, coast live oak also occurs in areas currently experiencing increased pressure from urban and agricultural development. Because of reduced habitat and regeneration problems, the factors that may be limiting natural replacement of oaks are of interest to land managers. In particular, potential factors affecting the most vulnerable stages in the oak life cycle, including the acorn and seedling stage, may provide information that will aid in maintaining current oak stands.

For acorns, the impact that insect feeding may have on germination is not well understood and may vary among oak species. Previous research suggests that insect damage to acorns may be a cause for limited natural germination of oak (Korstian 1927, Marquis and others 1976, Oliver and Chapin 1984, Weckerly and others 1989). While there is evidence that damaged acorns are still able to germinate (Walters and Auchmoody 1993), insect infestation of acorns may limit seedling vigor (Gribko 1995). It is not known how insect damage to acorns affects long-term vigor of seedlings and saplings. Tecklin and McCreary (1991) found that a larger acorn mass was positively associated with increased survival and height of blue oak, *Quercus douglasii* Hook. & Arn. A decreased mass of acorn reserves as a result of insect herbivory may reduce necessary reserves for seedling growth (Andersson 1992, Oliver and Chapin 1984). Artificial herbivory experiments confirm this trend, as acorns with more of the cotyledon removed are unable to survive when nutrient reserves are reduced (Kaushal and others 1993).

Defoliation of seedlings by herbivores has been implicated in areas with poor restoration success and is a potential causal mechanism for lowered natural regeneration, especially by damaging young leaf tissue (Tecklin and others 1997). Seedlings are affected more severely by herbivory than older saplings and mature trees, because relatively low levels of defoliation are sufficient to kill a seedling or trigger morphological changes to seedling leaves that result in decreased vigor (Larson 1978, Moller 1995, Moller and de Lope 1998). Additionally, herbivore damage to young seedlings can be detrimental to subsequent growth in some species of trees (McClaran 1985).

The specific impact that insect herbivory may have on juvenile oaks is poorly understood, but insect herbivory may be a factor in limiting the recruitment of seedlings to saplings. Several species of canopy- and seedling-feeding lepidopterans exhibit periodic increases in population sizes and have been shown to reduce survival of oak seedlings (Shaw 1974). The most common insects found feeding on oak seedlings in natural and restoration settings are grasshoppers (Adams and others 1991, Griffin 1971, McCreary and Tecklin 1994, McPherson 1993), which have been implicated as a causal factor in the failure of oak restoration efforts (McCreary and Tecklin 1994). In some areas, grasshopper damage has been significant enough to require insect barriers to prevent massive seedling mortality (Adams and others 1987, McCreary and Tecklin 1994). While southern California oak savanna habitats support many species of grasshoppers, the generalist feeder, *Melanoplus sanguinipes* (Fabricus), represents up to 95 percent of all grasshoppers collected in summer months (Porter and Redak 1997). This grasshopper is likely the most prevalent insect herbivore throughout the year in southern California oak woodlands (Porter and Redak 1997), and has the potential to consume large quantities of foliage, especially during years when population sizes are large (Capinera and Sechrist 1982).

Here we summarize two studies. The objectives of the first study (Acorn Study) were to determine (1.1) what insects are found feeding on acorns of *Q. agrifolia* and *Q. engelmannii* and what level of insect damage is present; (1.2) what the location of the insect-caused damage is on the acorns of both species; and (1.3) what the level of multiple infestation occurs in individual acorns. The objectives of the second study (Seedling Study) were to determine (2.1) the performance (as estimated by consumption and growth) of the generalist grasshopper, *M. sanguinipes*, feeding upon *Q. agrifolia* or *Q. engelmannii* seedlings; (2.2) if this grasshopper species shows a preference for either oak species; and (2.3) if herbivory by this species significantly damages either *Q. agrifolia* or *Q. engelmannii* seedlings.

Methods

Acorn Study

Emergence Traps

In order to identify adult weevils emerging from the ground beneath mature *Q. agrifolia* and *Q. engelmannii* trees, seven emergence cone traps (Raney and Eikenbary 1969) were placed underneath Engelmann and coast live oak trees at Santa Rosa Plateau Ecological Reserve (SRPER; 10 kilometers northwest of Temecula, California). Traps were placed under individual mature oaks (1 per tree) at randomly chosen locations underneath the canopy and were not moved throughout the study. Traps were initially placed in the field on April 20, 1999 and checked monthly for emerging weevils between April and September 1999.

One-month Emergence Trial

To identify individual and multiple accounts of insects infesting acorns from both *Q. agrifolia* and *Q. engelmannii* and to correlate amount and location of damage with particular insect species, a sample of 730 acorns from the 1998 acorn crop was collected in January 1999. Acorns were collected from two locations: SRPER and Southwestern Riverside County Multispecies Reserve (SWRCMSR; 20 kilometers northeast of Temecula, California). Acorns were collected from the ground beneath eight *Q. engelmannii* (n=530 acorns) and nine *Q. agrifolia* (n=200 acorns). Each acorn was placed into an individual rearing vial. Acorns were checked daily for emergence of larvae and parasitoids for a period of one month after collection.

After allowing one month for larvae to emerge, percent desiccation was estimated for each acorn, and all acorns were dissected to determine additional live and dead insect inhabitants, levels of multiple infestation and percent and type of damage (identified by weevil or lepidopteran frass). A ranking of insect-caused damage was applied to each acorn using the following damage-ranking scale of 0 to 6 (after Swiecki and others 1990): 0= no damage visible, 1= trace to 2.5 percent, 2= >2.5 percent to 20 percent, 3= >20 percent to 50 percent, 4= >50 percent to 80 percent, 5= >80 percent to 97.5 percent, and 6= >97.5 percent.

Monthly Samples

In July 1999, a second experiment was initiated to collect samples throughout the growing season from the 1999 acorn crop. These samples were collected to compare temporal variation in insect infestations, to further identify acorn inhabitants, and to determine the extent and location of damage to acorns. Samples (>30 acorns per tree) were taken from five *Q. agrifolia* and five *Q. engelmannii* trees (lower canopy) each month from August 1999 until the end of acorn fall in December 2000. A subsample of 20 acorns per tree was dissected and damage was ranked as above for each monthly sample. Location of damage (apical/basal) was also determined for every acorn.

Seedling Study

Seedlings of *Q. engelmannii* and *Q. agrifolia* were acquired from a local nursery in May 1999 and maintained throughout the experiment in a greenhouse at the University of California, Riverside. Grasshoppers (*M. sanguinipes*) were collected from SRPER on July 7, July 14, and August 1, 1999 and held in group cages with a diet of half wheat germ:half oat bran, iceberg lettuce, and sprouts until experiments began.

No-choice Experiment

To determine grasshopper performance and potential damage to both species of oaks, 30 *Q. agrifolia* and 30 *Q. engelmannii* seedlings were measured for total leaf area, then caged individually. After an initial starvation period of 24 hours, fourth-instar grasshoppers were weighed and then caged on each of the 30 *Q. engelmannii* and *Q. agrifolia* oak seedlings. At the end of the 20-day feeding period, all grasshoppers were removed and their fresh mass determined. Grasshoppers were then dried and weighed and all frass produced by each grasshopper during the trial was collected, dried, and subsequently weighed. Biomass gain of each grasshopper was estimated by subtracting initial dry masses from final dry masses. Grasshopper performance was measured by comparing final dry mass and biomass gain. We also compared the grasshoppers' utilization of both species of oaks. To determine the amount of grasshopper damage to both species of oak seedlings, amount of leaf biomass consumed was measured.

Choice Experiment

In order to determine grasshopper preference for either species, 20 pairs of *Q. engelmannii* and *Q. agrifolia* seedlings were measured for leaf area, and each pair placed into double acetate feeding chambers as above. Twenty grasshoppers were placed individually into feeding chambers containing a pair of oak seedlings. Extent of feeding damage was determined after 14 days by measuring the amount of leaf area consumed (original leaf area minus remaining leaf area). To determine if grasshopper preference was greater for either *Q. agrifolia* of *Q. engelmannii* seedlings, amount of leaf biomass removed was compared between the two species.

Results

Acorn Study

Identification of Acorn Inhabitants—All Collection Methods

The weevils collected from both the emergence trial and the monthly acorn samples were all larvae in the genus *Curculio*. None of the weevils collected from acorns became adults during the course of this research; consequently, identification to species was not possible; however; all adult weevils found in traps placed below mature trees were identified as *Curculio occidentis* (Casey) (Gibson 1969). Two species of lepidopteran larvae and adults found from the emergence trial and from the monthly samples were *Cydia latiferreana* (Walsingham) (Lepidoptera: Tortricidae) and *Valentinia glandulella* Riley (Lepidoptera: Blastobasidae). Several species of parasitoids were found throughout the study *(table 1)*. No cases of weevil parasitism were found in either species of oak acorns.

Table 1—*Parasitoids reared from Lepidoptera feeding on* Q. engelmannii *and* Q. agrifolia *acorns.*

Parasitoid	Host	Emergence date
Ichneumonidae		
Ctenopelmatinae (1)	*Q. engelmannii*	May 23
Pimplinae, (3)	*Q. agrifolia*	March 23
	Q. engelmannii	May 5
Braconidae		
Chelorinae, *Phanerotoma* sp. (1)	*Q. engelmannii*	March 15
Orgilinae, *Orgilus* sp. (2)	*Q. engelmannii*	January 14
Microgastrinae, *Dolichogenidea* sp. (1)	*Q. agrifolia*	April 16
Encyrtidae		
Copidosomatini, *Copidosoma evansi* (44)	*Q. engelmannii*	June 28

Emergence Traps

All weevils found in adult collection traps and on trees were identified as *Curculio occidentis.* Two weevil ovipositions were observed during the study. One female *Curculio occidentis* was observed ovipositing onto a *Q. agrifolia* acorn on October 14, 1999 and a second female was observed ovipositing onto an acorn of *Q. engelmannii* on October 29, 1999.

One-month Emergence Trial

Of the ground collected acorns, 62.3 percent exhibited some level of damage. Although the majority of all acorns were damaged, the level of damage was low (ranking of "1"= trace to 2.5 percent damage and "2"= >2.5 percent to 20 percent damage) for most acorns collected. A higher proportion of *Q. engelmannii* (58 percent) acorns were damaged than were *Q. agrifolia* (29 percent) acorns (χ^2= 46.8; $p<0.05$). A greater proportion of weevils, moth larvae and adults, and lepidopteran parasitoids were found within acorns of *Q. engelmannii* than in *Q. agrifolia.*

Insects emerged from 80 of 730 (11.0 percent) of the acorns collected. Of these, 117 weevil larvae emerged from 72 acorns, nine lepidopteran larvae emerged from nine acorns, and three additional lepidopteran larvae were parasitized. A total of eight out of 200 *Q. agrifolia* acorns in the rearing vials had insects emerge. After dissections, an additional 11 live weevils and 23 live lepidopteran larvae were found. Thirty-five dead weevils, seven dead lepidopteran larvae and 46 dead parasitoids (44 from one acorn) were found. A total of 111 acorns of *Q. engelmannii* contained weevils (21.0 percent of Engelmann acorns collected) and 41 acorns contained

Lepidoptera larvae and adults (7.7 percent); 39 *Q. agrifolia* acorns contained weevils. (19.5 percent of *Q. agrifolia* acorns collected), and only one *Q. agrifolia* acorn contained Lepidoptera larva (0.5 percent).

There were four co-occurrences of a *C. latiferreana* and a weevil within single *Q. engelmannii* acorns. No *Q. agrifolia* acorn sampled had both species inside. There were 68 occurrences of more than one *Curculio* sp. within a single *Q. engelmannii* acorn, and there were three occurrences of multiple *Curculio* sp. within single *Q. agrifolia* acorns *(fig. 1)*.

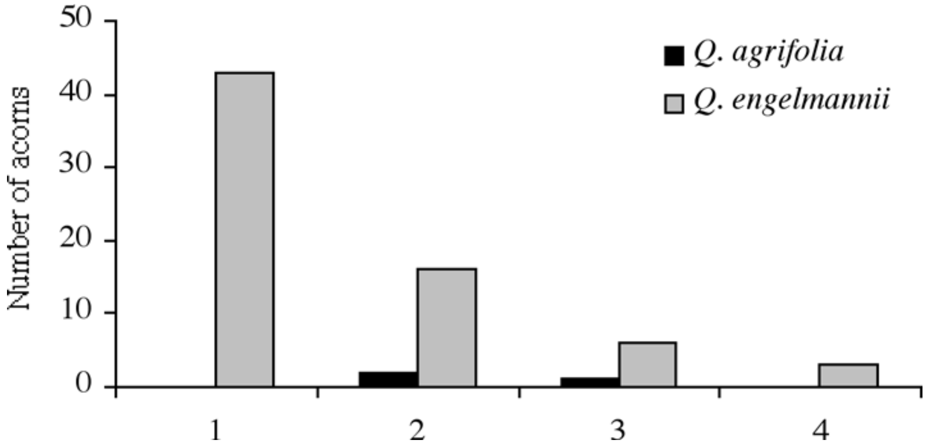

Figure 1—Number of acorns with different numbers of *Curculio* sp. weevils within a single acorn collected from ground samples in January 1999. Acorns collected were from the 1998 acorn crop.

Monthly Samples

In the subsequent July-December 1999 samples, overall damage to all acorns also was minimal (average damage rankings below 2), with no significant difference between the amount of damage found on subsampled *Q. agrifolia* and *Q. engelmannii* acorns (*t*-test; $t_{1,14}$= 1.4; p>0.05). The majority of damage to all acorns with over 50 percent damage was in the basal portion of the acorn for both oak species *(fig. 2)*, with, *Q. agrifolia* acorns exhibiting a higher proportion of basally damaged acorns (*t*-test; $t_{1,14}$= 3.2; p<0.05). The apical end of the acorn contains the growing embryo. There was no significant difference observed in the location of damage within Engelmann acorns (*t*-test; $t_{1,14}$= 1.4; p>0.05).

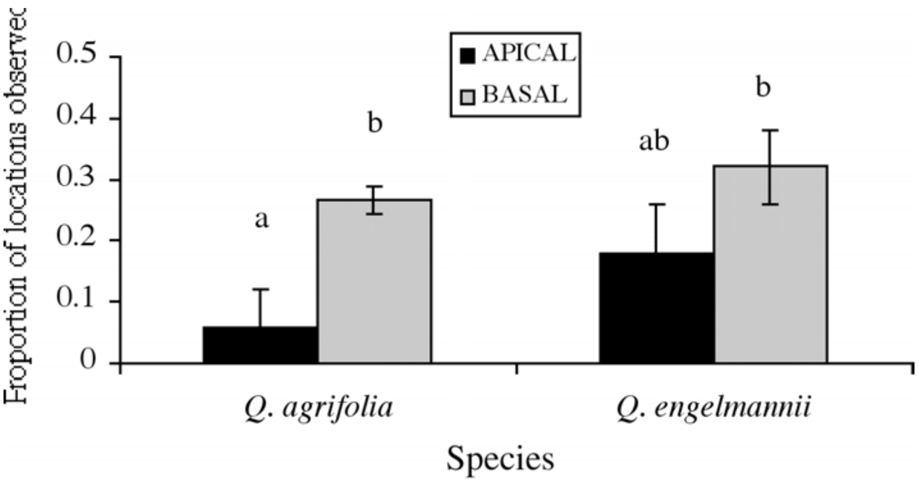

Figure 2—Proportion of *Quercus agrifolia* and *Q. engelmannii* acorns with apical and basal damage. Bars are means (±SE) for all acorns exhibiting over 50 percent damage from insects. Letters above bars indicate means are significantly different (t-test; $P<0.05$).

Numbers of oviposition scars peaked in late October 1999 for Engelmann acorns and August 1999 for coast live oak acorns. A significant amount of the variation in the number of weevil oviposition scars was described by the date of acorn collection for both *Q. agrifolia* ($F_{5,24}$= 5.4; $p<0.01$) and *Q. engelmannii* (*fig. 3*; $F_{5,24}$= 9.0; $p<0.001$). Date of collection also described a significant amount of the variation observed in insect damage for both species, with the amount of insect damage increasing seasonally ($F_{5,54}$= 9.6; $p<0.001$). The availability of acorns on each tree from which acorns were sampled (represented by a ranking of 0-6) was not a significant predictor of the number of weevil ovipositions observed for either species (Analysis of variance [ANOVA] for *Q. agrifolia*; $F_{5,24}$= 0.8; $p>0.05$; ANOVA for *Q. engelmannii*; $F_{3,26}$= 0.7; $p>0.05$).

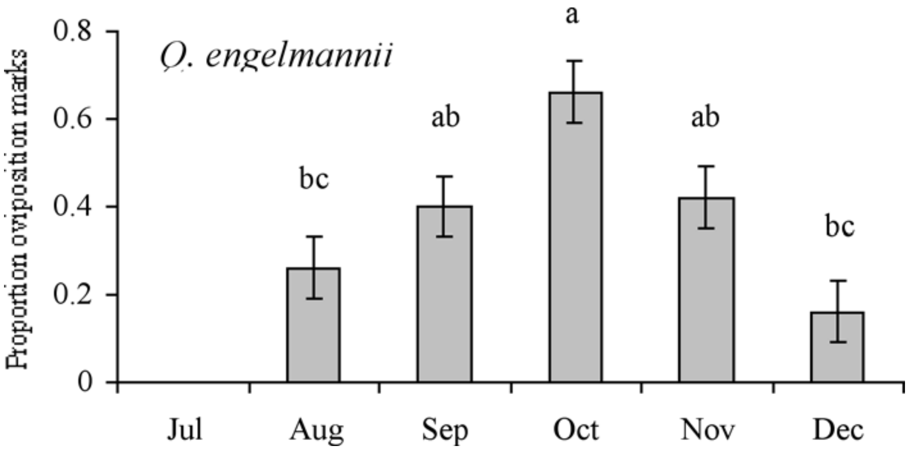

Figure 3—Average *Curculio* sp. oviposition marks per acorn found on acorns collected from *Quercus agrifolia* and *Q. engelmannii* in July through December 1999 samples. Values shown are least square means (±SE; n=5/month). Different letters above bars indicate means are significantly different among species (Ryan-Einot-Gabriel-Welsch multiple-range test ANOVA; $P<0.05$)

Seedling Study

No-choice Experiment: Grasshopper Performance

Grasshoppers feeding upon *Q. engelmannii* gained significantly less biomass than those feeding upon *Q. agrifolia* (Analysis of covariance [ANCOVA]; $F_{1,47}$= 18.6; p<0.001); in fact, they actually lost biomass over the course of the 20-day experiment. There was no significant interaction between initial biomass and the grasshopper biomass gained ($F_{1,46}$= 1.9; p>0.05).

Grasshoppers feeding on either oak species produced equivalent amounts of frass once the total amount consumed had been taken into account (ANCOVA; p>0.05). Analysis of covariance, with biomass consumed as a covariate, did not indicate a difference between tree species.

No-choice Experiment: Damage to Seedlings

Q. agrifolia seedlings in the feeding trials had more available leaf mass than the same age *Q. engelmannii* seedlings. Once effects of initial insect mass and availability of seedling biomass were removed, more *Q. agrifolia* seedling leaves were damaged than *Q. engelmannii* leaves (ANCOVA; p<0.001). Plant size was not a factor affecting herbivory. Grasshoppers preferred to feed upon *Q. agrifolia* seedlings, regardless of the available seedling biomass associated with each species of seedlings. As with the preceding analyses, there were no interaction effects between treatment and the covariate of initial plant mass ($F_{1,49}$= 2.0; p>0.05) or the covariate of initial grasshopper mass ($F_{1,49}$= 1.2; p>0.05).

Choice Experiment: Grasshopper Preference

After adjusting for the biomass of seedlings available for consumption, grasshoppers preferred to consume more *Q. agrifolia* biomass (ANCOVA; p<0.001). As in the no-choice trials, grasshoppers did not prefer to feed upon seedlings with greater biomass available (ANCOVA; p>0.05). There was no significant interaction between the biomass of seedlings initially available and the mass of leaves consumed by the grasshoppers ($F_{1,36}$= 2.9; p>0.05).

Discussion

Acorn Study

While the larvae were not confirmed to be *Curculio occidentis* and did not pupate during the course of the research, the occurrence of the adults of this species in the collection traps indicates that this species uses both *Q. agrifolia* and *Q. engelmannii* as a host and that the collected larvae are likely this species as well. The observation of females ovipositing on acorns of both oak species further confirms the association of *C. occidentis* with both species of oaks. *Curculio occidentis*, *C. latiferreana,* and *V. glandulella* are all listed in the most recent edition of the California Oak Disease and Arthropod (CODA) Database (Swiecki and others 1997a) and are cited as herbivores of *Q. agrifolia*. This study confirms their association with *Q. engelmannii* as well. The two moths, *Cydia latiferreana* and *V. glandulella*, are common among oak species, with the latter most commonly detected as a secondary pest feeding on acorns that have been previously damaged by *Curculio* sp. (Bonner and Vozzo 1987). *Valentinia glandulella* also has been found to feed on undamaged acorns (Galford 1986). In the current study, this species was both a primary herbivore (found feeding with no other previous damage observed) and a secondary herbivore (found feeding on previously damaged acorns).

The majority of acorns studied in the emergence trial were damaged; however, the total damage to each acorn was slight. During the one-month emergence trials, insects emerged from only 10 percent of all acorns collected. Despite the discovery of insects within acorns after dissections, the total number of insects found remained small. As all acorns in the emergence trial were collected from the ground in January, the level of insect damage observed and the number of insects collected represents a bias towards acorns not taken by vertebrates. Vertebrate herbivores were not excluded from the areas where acorns were collected. Thus, depending upon the acorn foraging preferences of vertebrates, the actual percentage of insect damaged acorns from the entire crop of acorns may be incorrectly estimated. In the subsequent monthly sampling period of acorns collected from the canopy, the extent of damage to each acorn examined matched the results found in the one-month emergence trial. There was no significant difference between the two species of oaks in damage incurred by insects.

Percentage of damaged acorns has been observed to be as high as 80 percent within one stand of oaks (Scutareanu and Roques 1993). In Marin county, northern California, Lewis (1991) found 25 percent of *Q. agrifolia* acorns sampled had signs of insect boring activity. Out of 501 acorns dissected, 38 percent had signs of insect damage; 70 percent were damaged by a *Curculio* sp. and 30 percent were damaged by the filbertworm. Swiecki and others (1991) found up to 47 percent of some *Q. douglasii* samples with *Curculio* sp. and 60 percent with *C. latiferreana*. We found 21 percent of ground-collected *Q. engelmannii* acorns contained *Curculio* sp. weevil larvae and 8 percent contained lepidopteran larvae. The number of ground-collected *Q. agrifolia* acorns containing weevil larvae was 20 percent and 0.05 percent contained lepidopteran larvae. Number of insects from this study are lower than numbers found in other studies; however, the number of damaged acorns was much higher and these numbers represent only ground-collected acorns from one season. Insect damage levels to oaks in California vary with yearly acorn production among and within trees from year to year (Koenig and others 2002). Acorn surveys at the Santa Rosa Plateau indicate that the 1998 acorn crop for Engelmann was high, while the acorn crop for coast live oak was fair. The 1999 acorn crop was determined to be better than average for coast live oak and a low acorn year for Engelmann oak. The year to year variation observed in acorn numbers may impact the numbers of infested acorns found. Because of the annual variability that exists in the numbers of acorns produced and the insects feeding on them, insects may have a significant impact on this oak system (Swiecki and others 1991).

The damage observed to the acorns resulted from larval tunneling throughout the acorn. Several of the acorns collected in this study showed no external signs of insect damage, yet had signs of insect tunneling beneath the pericarp. The majority of both ground-collected and canopy-collected acorns were significantly more damaged in the basal, or cap end, portion of the acorn than in the apical, growing end of the acorn; however, the proportion of damage that was apical was higher for *Q. engelmannii*. This has implications for the potential for Engelmann oak acorns to germinate after being partially damaged. If the apical, or growing embryo tip, of the acorn is damaged, then the potential for germination is reduced (Bonner and Vozzo

1987). Previous research has suggested that granivores preferentially feed upon the basal portion of acorns to avoid a higher tannin concentration in the growing tip (Steele and others 1993). Although no plant chemistry was described for either species in this study, the majority of damage seen was in the basal portion for both species.

Only 4 of 750 (0.5 percent) acorns in emergence trials contained more than one insect species feeding within the same acorn. *Cydia latiferreana* and a *Curculio* sp. were the two species found together within single acorns. Co-occurrence of both a *Cydia* sp. and a *Curculio* sp. larva within a single nut also has been observed in previous studies of oak and chestnut systems (Lewis 1991, 1992; Swiecki and others 1991; Debouzie and others 1993; Arahou 1994). Arahou (1994) found that of 30 acorns with both *Curculio glandium* Marsham and *Cydia fagiglandana* Z., no acorns germinated. Less than 1 percent of acorns sampled contained more than one species of insect feeding upon a single acorn, while 4 percent contained multiple *Curculio* sp. larvae. The occurrence of multiple infestation of single species within a single nut has been observed for many *Curculio* sp., with numbers as high as eight weevils per acorn occurring in northern California (Swiecki and others 1991). Although not common, this has also been observed in both *Q. engelmannii* and *Q. agrifolia*.

The number of insect-damaged acorns found in this study suggests that insects, mainly *Curculio* sp. weevils and lepidopteran larvae, have the potential to damage high numbers of *Q. agrifolia* and *Q. engelmannii* acorns in southern California. Although the average amount of damage observed on each acorn was minimal, the damage inflicted by these insects and how it may impact subsequent seedling growth is unknown, but potentially significant. Germination tests with damaged acorns are required to determine the impact that insect damage has on seedling growth

Seedling Study

Grasshoppers preferred seedling leaves of *Q. agrifolia* over *Q. engelmannii*. Grasshopper herbivory to live oak seedlings may be a more important limiting factor to their successful regeneration than herbivory to Engelmann oak. *Quercus agrifolia* also may be more susceptible than *Q. engelmannii* to other generalist insect herbivores associated with southern California woodlands.

Quercus agrifolia was preferred over *Q. engelmannii* in the choice test and was a superior host plant as evidenced by greater insect growth in the no-choice tests. When provided with only *Q. engelmannii*, *M. sanguinipes* lost biomass and grew significantly less than animals provided with only *Q. agrifolia*. *Quercus engelmannii* is a poor diet for grasshoppers; its suitability as a host plant for other insect herbivores remains to be documented. The difference in feeding performance and preference may be a result of different chemical compositions in the leaves (Feeny 1970). While previous research has identified chemical composition of *Q. agrifolia* leaves, information about the chemical components in the leaves of *Q. engelmannii* is lacking and further research is needed before a discussion of chemical differences can be applied to the results presented here.

Our results suggest that care should be taken to monitor and/or control grasshoppers in *Q. agrifolia* restoration and replanting areas. This study demonstrated coast live oak to be a relatively adequate food source for a common grasshopper found throughout southern California habitats where current (and future) oak restoration and planting occur. By monitoring the annual population fluctuations of this species, potential damage to newly planted seedlings could be prevented before severe levels of defoliation occur. *Quercus engelmannii*, however, does not appear to provide a sufficient diet for *M. sanguinipes*, suggesting that even with large numbers of grasshoppers, *Q. engelmannii* may receive less grasshopper damage than *Q. agrifolia*.

Coast live oak seedlings have been shown to experience higher mortality than co-occurring species when subjected to simulated herbivory (Muick 1997). Seedlings of *Q. agrifolia* in the Central Valley of California had a reduced survival relative to *Q. douglasii* when subjected to clipping treatments. Following 104 oak seedlings in central coastal California over a 4-year period, White (1966) found an 88 percent survival rate of *Q. douglasii* seedlings, with no *Q. agrifolia* surviving.

In contrast, coast live oak saplings have a much higher success rate with resprouting following herbivory (Griffin 1971, Pillsbury and Joseph 1991); however, acorns or young seedlings, rather than saplings, are usually planted in restoration projects. Because these seedlings are preferred by grasshoppers, herbivory to coast live oak seedlings may greatly impact restoration efforts in southern California.

Given a choice between *Q. engelmannii* and *Q. agrifolia* seedlings in a greenhouse setting, *M. sanguinipes* both preferred and performed better on *Q. agrifolia*. Seedlings of *Q. engelmannii* are apparently not a suitable host for *M. sanguinipes* as evidenced by the loss in biomass resulting during the feeding trials. This suggests that *M. sanguinipes* has the potential to defoliate newly planted *Q. agrifolia* seedlings, but is unlikely to affect *Q. engelmannii*. This study also suggests that greater attention be given to grasshoppers and other invertebrates as potential herbivores in plantings of oak seedlings.

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Rooting and Foraging Effects of Wild Pigs on Tree Regeneration and Acorn Survival in California's Oak Woodland Ecosystems[1]

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Abstract

Wild pigs (*Sus scrofa*) have been widely distributed by humans and significant populations now occur in oak-dominated ecosystems in California. Because they are omnivorous and forage by rooting, wild pigs have the potential to impact a wide variety of plants and animals directly by consumption and indirectly through disturbance. In 1998, we initiated a long-term study of the ecological effects of wild pigs on oak woodland ecosystems in California using multiple exclosures with paired control plots targeting four oak communities in the north and central coast region of California that vary in population density of wild pigs. Soil disturbance by wild pigs was significantly higher in areas where wild pig densities are high. Rooting significantly reduced aboveground plant biomass in oak grassland and oak woodland habitats, and may therefore reduce forage availability for herbivores in areas with widespread rooting. Rooting disturbance may be significantly reducing survival of tree seedlings, thereby limiting tree regeneration in oak woodlands. Experimental plots associated with high masting oak trees indicated that wild pigs significantly reduced acorn survival and, therefore, reduced the availability of acorns for germination and consumption by native wildlife.

Introduction

Pigs (*Sus scrofa*) are a large ungulate native to Eurasia and North Africa, and are now widely distributed as feral animals in many areas including California (Oliver and Brisbin 1993). Wild pigs in California originated from domestic pigs foraging on acorns in oak woodlands around Spanish settlements in the late 1700s (Mayer and Brisbin 1991). They have expanded significantly in California in recent years related to a combination of hunting-related introductions, spread of agriculture, releases of domestic swine by hog farmers, and natural dispersal (Waithman and others 1999). Although wild pigs are popular among sport hunters, expanding populations increasingly conflict with agricultural and conservation activities by crop depredation and rooting disturbance in natural areas (Giusti 1993).

Previous studies of wild pigs in mainland California have provided information on aspects of the population ecology of wild pigs (Barrett 1978, Schauss and others 1990), but little quantitative information is available on the effects of wild pigs on the oak-dominated regions they occupy (Kotanen 1995). In 1998 we initiated a large-

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scale study of the ecological effects of wild pigs in oak woodland ecosystems. Research began in May 1998 and will be continuing through October 2004. The primary objectives of the study are to assess the effects of rooting and foraging by wild pigs on (1) regeneration potential of oak trees, and (2) diversity and abundance of native and nonnative plants and terrestrial vertebrates (small mammals, reptiles and amphibians). In 1998 and 1999 we established multiple fenced exclosure and control plots at research sites in the central and north coast regions of California to begin to evaluate hypotheses about how rooting and other activities of wild pigs impinge on oak woodland ecosystems. A variety of activities is underway *(table 1)*; here we will focus on research assessing how rooting and foraging by wild pigs influences tree regeneration and forage availability for native wildlife.

Table 1—*Summary and description of different research activities being used to assess the effects of wild pig rooting and foraging activities on oak woodland ecosystems in California.*

Activity	Brief description	Target organisms/purpose
Rooting transects	100 m line transects with five 2 m^2 quadrats, one every 20 m	Plants - vegetative cover and biomass production
Oak canopy experiments	3x3 m fenced exclosures with four 1x1 m acorn monitoring plots nested within	Acorns - acorn survival rates and regeneration potential
Tree seedling transects	40x4 m line transects, some nested within fenced exclosures	Oaks, conifers, woody shrubs - regeneration
Mammal trapping	7x7 trap grids 7-8 m spacing, some grids enclosed by fenced exclosures	Small rodents - species list, species richness and diversity, relative abundance
Pitfall arrays	Y-shaped arrays composed of a central trap and three arms with three traps along each arm. Some arrays within fenced exclosures	Rodents, amphibians, reptiles, invertebrates - species lists, species richness and diversity, relative abundances
Timed searches	30 minute time-constrained searches for reptiles and amphibians	Reptiles, amphibians - species lists, species richness and diversity, relative abundances
Coverboards	transects along drainages each with 20 coverboards (0.6x0.6 m) spaced every 20 m	Amphibians, reptiles - species lists, species richness and diversity, relative abundances
Vegetation plots	2x2 m plots, some nested within fenced exclosures	Native, nonnative grasses - species lists, species richness and diversity, relative abundances

Study Areas

Introduced wild pigs may or may not negatively influence ecological processes operating in mainland ecosystems, except perhaps in areas with relatively high-density populations (Sweitzer 1998). Thus, research sites selected for this study were focused in several relatively small areas of the central and north coast regions of California where high-density wild pig populations are centered (delineated in Waithman and others 1999). Within these regions, study sites were further restricted to (1) areas without free-ranging livestock because cattle grazing may interfere with efforts to assess the effects of wild pigs, (2) areas where control activities provided opportunities for comparative research between a site with ongoing wild pig control and a nearby site without wild pig control, and (3) sites where we were allowed to construct small exclosures as part of experimental comparisons. In the north coast region of the state we established three research sites in summer 1998; Austin Creek State Recreation Area (Austin Creek SRA, western Sonoma County), Sugarloaf Ridge State Park (Sugarloaf Ridge SP, eastern Sonoma County), and the McCormick Sanctuary (eastern Sonoma County). In summer 1999 Henry Coe State Park (Henry Coe SP, Santa Clara County) in the central coast region of the state was added to the study. Austin Creek SRA and Henry Coe SP were experimental sites where different types of fenced exclosure plots were established to allow for direct experimental evaluation of pig effects. Sugarloaf Ridge SP was a site with long-term and ongoing wild pig control, and McCormick Sanctuary was a site with no organized wild pig control, located immediately to the north of Sugarloaf Ridge SP. Sugarloaf Ridge SP and McCormick Sanctuary were considered comparative research sites, with data collected at Sugarloaf Ridge SP compared to those from McCormick Sanctuary.

Methods

Habitat Plots and Exclosures

Several research activities were focused around habitat plots and/or exclosures established in oak grasslands, oak woodlands, mixed forests, and meadows. At each experimental research site we established four large 50x50 m fence exclosures designed to allow foraging access by all herbivores except wild pigs. Exclosures were built by wiring 0.9 m high field fence to 1.9 m fence posts driven into the ground every three meters. Rebar stakes secured fencing to the ground between posts. The low height of the field fence and large mesh openings (10x10 cm) allowed deer and small vertebrates to easily enter. For each exclosure, we also staked out a matched 50x50 m control plot, usually within 500 m of the exclosure. Nested within each 50x50 m exclosure and control habitat plot were (1) a 7x7 small mammal live trap grid, (2) six 4x40 m seedling belt transects, (3) a y-shaped pitfall trap array with 10 traps, and (4) several 2x2 m vegetation plots near each of the four corners. Details and data on small mammal trapping, pitfall trapping, and vegetation plot analyses will not presented in this paper due to space constraints.

Exclosures at Austin Creek SRA were located in four different habitats: oak grassland, oak woodland, mixed woodland, and riparian meadow. At Henry Coe SP two exclosures each were established in oak woodland and oak grassland habitats. At both Sugarloaf Ridge SP and McCormick Sanctuary, 50x50 m plots were staked out in four different types of habitat (oak grasslands, oak woodlands, mixed woodlands, and riparian meadows). Plots in each habitat at Sugarloaf Ridge SP and McCormick Sanctuary were carefully surveyed prior to establishment so as to match them ecologically and thereby allow for research comparisons.

Rooting Dynamics

We characterized the extent of wild pig rooting disturbance at all research sites using quadrat sampling along 100 m “rooting transects.” During the spring periods of 1999 and 2000, 14 to 20 100-meter rooting transects were surveyed at each research site within oak grassland and oak woodland habitats. For each 100-m line transect randomly situated within the appropriate habitat types, five 2.0 m^2 quadrats (PVC pipe frame) were randomly placed from 1 to 10 meters to the left or right side of the transect line at 20 meter intervals. For each quadrat we noted the presence or absence of rooting, and prepared scaled down line drawings of rooted areas when rooting was present. During 1999, two of five quadrats along each rooting transect were randomly selected for sampling of total biomass production by clipping all nonwoody vegetation to ground level. Because this approach resulted in relatively few biomass samples from quadrats that were rooted, we altered our biomass sampling protocol for summer 2000. During summer 2000 we estimated biomass productivity in relation to rooting by randomly selecting two of the five sampling intervals (20, 40, 60, 80, 100 meters) along each 100-m rooting transect for biomass sampling. At the two randomly selected intervals, we laid out a 10-m tape to the left or right and perpendicular to the 100-m rooting transect. We then placed the edge of a 2 m^2 quadrat at the point at which the tape first intersected wild pig rooting, prepared a scaled down line drawing of rooting in the quadrat, and sampled all aboveground biomass by clipping nonwoody vegetation to ground level. Next, we established a 2 m^2 control biomass quadrat in an unrooted area, as near as possible to the rooted biomass quadrat, and matched to the dominant vegetation in nonrooted areas of the rooted quadrat. This control biomass quadrat was also sampled for aboveground biomass. Clipped vegetation was dried to constant weight for determination of dry matter biomass. For data from 1999, analyses were by linear regression of log transformed dry matter biomass by the estimated proportion of rooting in biomass plots. Data from 2000 were analyzed by linear regression of arcsin transformed proportional differences in dry matter biomass between matched rooted and control biomass plots against percent rooting disturbance in the rooted biomass plots.

Regeneration Potential in Oak and Mixed Forest Woodlands

Rooting by wild pigs may reduce tree regeneration by damaging or uprooting young seedlings. We used three different approaches to assess this hypothesis: (1) comparisons of data on tree seedling sizes along multiple 4x40 m "belt transects" in oak woodland and mixed forest habitats at all research sites, (2) comparisons of data on tree seedling size and number along belt transects in 50x50 m exclosure and control habitat plots in oak woodland and mixed forest areas at experimental research sites, and (3) comparison of numbers and sizes of tree seedlings in 3x3 m oak canopy exclosure and control plots, also at experimental research sites.

Belt transects were initiated at selected starting positions within continuous tracts of oak or mixed woodland. From starting positions for each belt transect, we randomly selected an azimuth from 0 to 359 degrees N and laid out a 40 m line transect. All tree seedlings encountered within two meters of either side of the tape were identified and measured from ground level to the terminal bud. A moveable 2x4-m rope frame was used to facilitate sampling seedlings along the 40-m transect line. As part of analyses of seedling data, we calculated an index to regeneration potential, defined as the ratio of large seedlings (>200 mm) to total seedlings, for each belt transect. A low regeneration index suggests that relatively few tree seedlings survived to a relatively large size where they may be less prone to mortality by rooting. Data on arcsine transformed regeneration indices were evaluated by analysis of variance (ANOVA).

At Austin Creek SRA and Henry Coe SP, additional belt transects in paired 50x50 m exclosure and control habitat plots in oak woodland and mixed woodland areas (Austin Creek SRA only) were used to experimentally assess effects of wild pig rooting on tree regeneration. Within the habitat plots, we defined six 4x40-m belt transects situated between and parallel to the 7x7 small mammal trap grid lines. During summer 2001 all exclosure and control belt transects were surveyed for tree seedlings. Data on log transformed seedling sizes and average numbers of seedlings noted along belt transects in paired exclosure and control habitat plots were evaluated by ANOVA. As part of oak canopy exclosure experiments described below, we also counted and measured all tree seedlings located in each oak canopy exclosure and paired control plot at Austin Creek SRA and Henry Coe SP during spring 2000 and spring 2001. Data on sizes and numbers of seedlings collected from oak canopy experiment plots also were evaluated by ANOVA.

Oak Canopy Experiments

Acorn consumption by wild pigs may reduce resource availability for native wildlife, while simultaneously limiting oak regeneration by consumption of acorns that might otherwise germinate. We tested these hypotheses with exclosure experiments beneath canopies of high acorn mast producing oak trees at Austin Creek SRA in 1998 and 1999 and Henry Coe SP in 1999. The design of "oak canopy experiments" included (1) mid-summer surveys of oak woodlands for high acorn producing oak trees (Category four acorn producers, Graves 1980), (2) establishing small 3x3m exclosure and control plots beneath the canopies of selected oak trees, and (3) monitoring numbers of acorns present on two 1x1m monitoring plots within each exclosure and control plot from mid-September to mid-December. Sixteen high-masting oak trees were selected for oak canopy experiments at Austin Creek SRA in 1998 (14 *Quercus kelloggii,* two *Lithocarpus densiflorus*). In 1999 at Austin Creek SRA, 5 of the 15 oak trees from 1998 (three *Q. kelloggii*, two *L. densiflorus*) retained sufficient acorns to continue acorn monitoring, and an additional 10 high masting trees were identified and selected for experiments, including two *Q. kellogii*, five *Q. agrifolia*, two *Q. lobata*, and one *Q. garryana.* Fifteen high-mast-producing oak trees were selected for experiments at Henry Coe SP in 1999: seven *Q. douglasii*, three *Q. agrifolia*, four *Quercus lobata*, one *Q. garryana*).

At each selected oak tree, exclosure and control designations were randomly assigned to each of two 3x3-m plots marked out beneath portions of tree canopies with approximately similar numbers of acorns (estimated visually). Exclosures for the experimental plots were built using the same design features as habitat plot exclosures. Control canopy plots were delineated by a single 1.9-m fence post at each corner. Within each exclosure and control plot, two 1x1-m acorn survival monitoring plots were staked out using short lengths of metal rebar. Beginning in mid-September and continuing until mid-December, the numbers of acorns present on acorn survival plots were assessed every 2-3 weeks. During periodic acorn counts, we discriminated between acorns from previous years and current-year acorns, and between immature and mature current-year acorns. We also recorded evidence of acorn foraging by wild pigs and other wildlife.

Results

Rooting Disturbance

Sixty-eight and 81 rooting transects were used to estimate wild pig rooting disturbance in oak grassland and oak woodland habitats during 1999 and 2000, respectively. Based on presence or absence of rooting in 2 m^2 quadrats along rooting transects, rooting was more widely distributed at research sites with relatively high densities of wild pigs (Austin Creek SRA, Henry Coe SP) compared to sites with low densities of wild pigs (Sugarloaf Ridge SP, McCormick Sanctuary). In 1999 the proportions of 2 m^2 quadrats with rooting along transects in all habitats ranged from 10 percent at Sugarloaf Ridge SP to 79 percent at Henry Coe SP ($\alpha<0.001$). Similarly, in 2000 the proportions of 2 m^2 quadrats rooted along transects in all habitats ranged from 13 percent at Sugarloaf Ridge SP to 92 percent at Henry Coe SP ($\alpha<0.001$). Analyses of line drawings of rooting disturbance in 2 m^2 quadrats in oak grasslands suggested that area rooted by wild pigs in 1999 was much lower at Sugarloaf Ridge SP compared to the other research sites (*fig. 1*; $\alpha<0.001$). In oak grassland habitats in 2000, however, less area was rooted at Sugarloaf Ridge SP and McCormick Sanctuary compared to Austin Creek SRA and Henry Coe SP (*fig. 1*; $\alpha<0.001$). There was less rooting in oak woodland habitats in 1999 at Sugarloaf Ridge SP and McCormick Sanctuary compared to both Austin Creek SRA and Henry Coe SP (*fig. 1*; $\alpha<0.001$). Also, rooting in oak woodland habitats in 1999 at Austin Creek SRA was higher than at Henry Coe SP *(fig. 1)*. In 2000 there was less rooting in oak woodland habitats at Sugarloaf Ridge SP and McCormick Sanctuary than at Austin Creek SRA and Henry Coe SP (*fig. 1*; $\alpha<0.001$). Also, in 2000 more area was rooted in oak woodlands at Henry Coe SP than at Austin Creek SRA *(fig. 1)*.

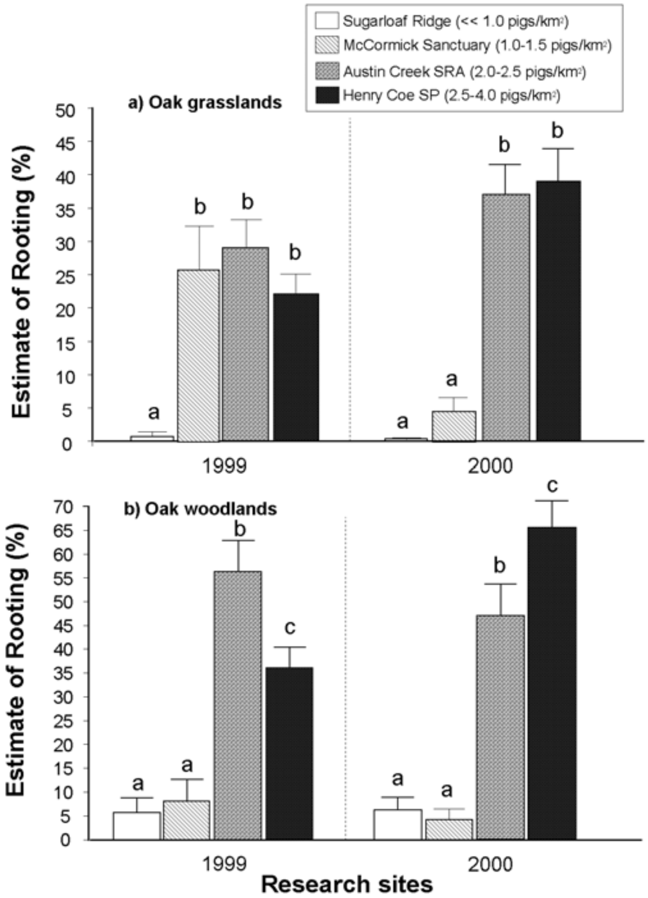

Figure 1—Data on rooting disturbance by wild pigs in (a) oak grassland and (b) oak woodland habitats at the different research sites during the study. Error bars are 1 SE. Different letters between bars indicate significant differences ($\alpha<0.05$).

Data on the effects of rooting on aboveground plant biomass were collected in different ways in 1999 and 2000. For 1999, linear regression analyses of data on natural log transformed dry matter plant biomass by the proportion of a quadrat rooted revealed similar negative relationships between rooting disturbance and aboveground biomass in oak grasslands and oak woodlands *(fig. 2)*. Similarly, linear regression relationships for data from Spring 2000, indicated that as rooting disturbance increased, dry matter plant biomass in rooted biomass plots decreased relative to dry matter plant biomass in unrooted control plots in the same quantitative fashion in grasslands and woodlands *(fig. 2)*.

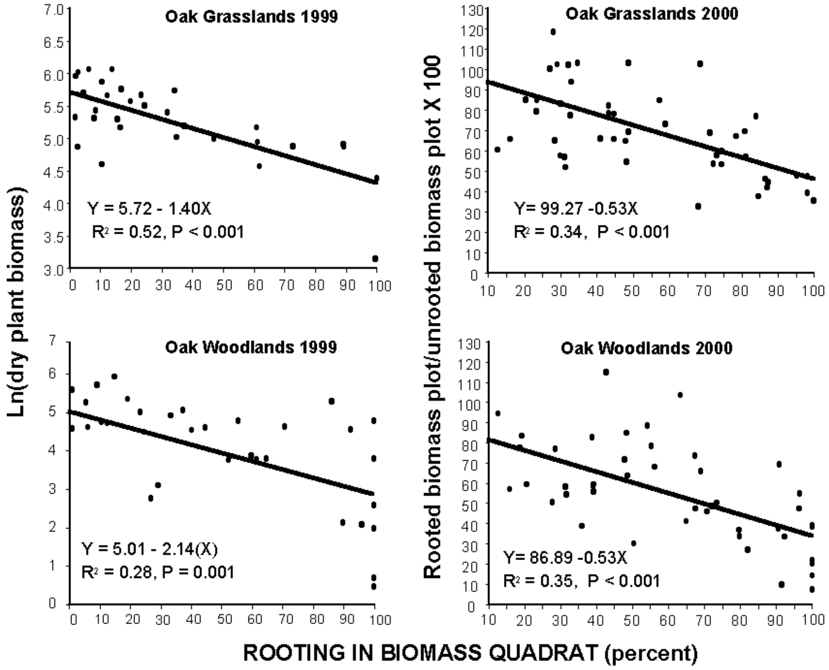

Figure 2—Linear regression relationships between rooting disturbance and aboveground dry plant biomass in oak grassland and oak woodland habitats from 1999 and 2000. Rooting effects on plant biomass were assessed differently in 1999 and 2000.

Tree Regeneration in Oak and Mixed Woodland Habitats

In 1999 and 2000 we measured a combined 15,875 tree seedlings along 80 linear belt transects in oak woodland habitats and 7,385 tree seedlings along 35 linear belt transects in mixed woodland habitats at the four research sites *(table 2)*. Analyses revealed significant variation in mean tree regeneration indices in oak woodland habitats among research sites ($\alpha<0.001$), related to fewer large tree seedlings at sites with higher densities of wild pigs *(fig. 3)*. Pairwise comparisons indicated a higher mean tree regeneration index for Sugarloaf Ridge SP compared to McCormick Sanctuary, Austin Creek SRA and Henry Coe SP (α's<0.028). Tree regeneration indices in oak woodland habitats were similar at the other three research sites. Considering oak tree seedlings only, there also were significant differences in mean tree regeneration indices among research sites ($\alpha=0.001$), related to progressively lower mean oak tree regeneration indices at research sites with increasingly higher wild pig densities *(fig. 3)*. In mixed woodland habitats, however, there was no apparent variation in tree regeneration indices among sites for all tree seedlings (α=0.84, *fig. 3*), or oak tree seedlings only (α=0.10).

Table 2—*Summary of data on tree seedlings enumerated along seedling belt transects in oak woodland and mixed woodlands habitat at each study site during 1999 and 2000.*

	Seedling transects	Total oak seedlings	Large oak seedlings[1]	Total tree seedlings[2]	Large tree seedlings
Oak woodlands 1999					
Sugarloaf Ridge SP	10	569	61	1,266	223
McCormick	10	1,884	83	3,049	244
Austin Creek SRA	10	2,131	28	2,517	58
Henry Coe SP	10	528	19	612	24
Mixed woodlands 1999					
Sugarloaf Ridge SP	5	70	12	1,008	167
McCormick	5	117	26	2,407	457
Austin Creek SRA	5	83	4	423	62
Oak woodlands 2000					
Sugarloaf Ridge SP	10	1,288	129	2,012	415
McCormick	10	2,584	54	3,383	171
Austin Creek SRA	10	1,965	28	2,741	181
Henry Coe SP	10	226	11	295	27
Mixed woodlands 2000					
Sugarloaf Ridge SP	5	150	13	949	234
McCormick	5	231	104	1,435	192
Austin Creek SRA	5	201	6	738	147
Henry Coe SP	5	313	35	435	83

[1] Large tree seedlings were defined as seedlings >200 mm in total size.

[2] All tree seedlings includes oak, conifer, and other hardwood tree seedlings.

Data on tree seedlings along belt transects in habitat exclosure and control plots at Austin Creek SRA and Henry Coe SP were analyzed separately because exclosures were set up one year earlier at Austin Creek SRA. After nearly three years of protection from wild pigs, there were over twice as many tree seedlings along six belt transects in the oak woodland exclosure habitat plot (n=4,869) compared to along six belt transects in the oak woodland control habitat plot (n=2,007) at Austin Creek SRA. Tree seedlings in the oak woodland exclosure habitat plot averaged 96.0 ±0.9 mm compared to 87.0 ±1.7 mm in the oak woodland control habitat plot (α<0.001). In mixed woodland habitat plots at Austin Creek SRA there were nearly twice as many tree seedlings along six belt transects in the exclosure plot (n=1409) compared to along six belt transects in the control plot (n=882). Tree seedlings in the mixed woodland exclosure habitat plot, averaged 98.7 ±2.6 mm compared to 146.5 ±5.9 mm in the mixed woodland control habitat plot (α=0.001). Exclosure habitat plots at Henry Coe SP have been established for two years, but the numbers of seedlings along belt transects in the oak woodland exclosure habitat plots (n=638) were approximately similar to the numbers located along belt transects in oak woodland control habitat plots (n=571). Similarly, the mean sizes of tree seedlings in oak woodland exclosure habitat plots (77.0 ±2.3 mm) were similar to the mean sizes of those in oak woodland control habitat plots (86.9 ±4.7 mm; α=0.10).

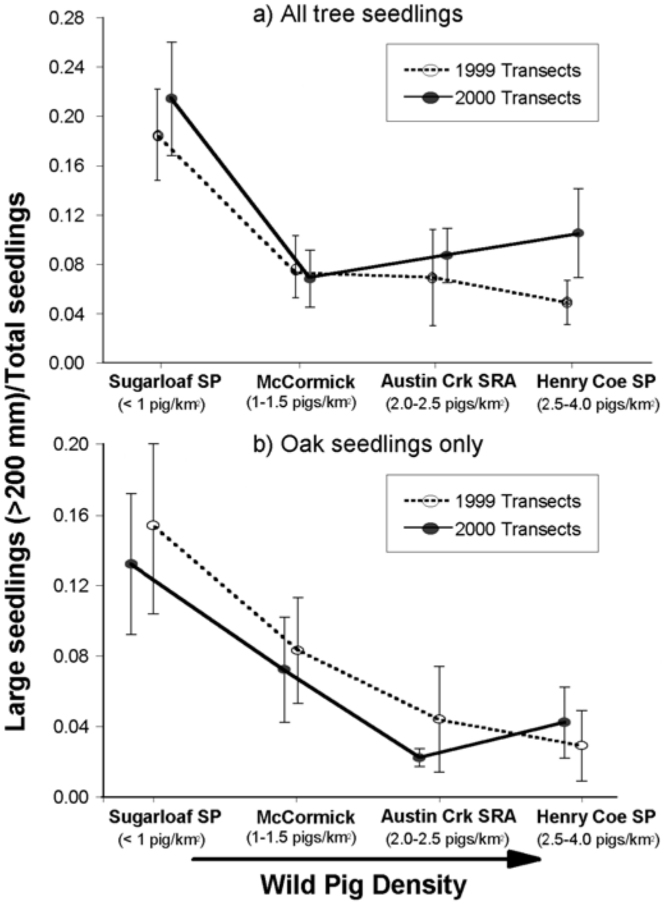

Figure 3—Variation in tree regeneration indices calculated for (a) all tree seedlings, and (b) oak tree seedlings based on data from belt transects at the different research sites.

Data on seedlings in oak canopy exclosure and control plots for experimental oak trees at Austin Creek SRA (*n*=21 trees) and Henry Coe SP (*n*=15 trees) were analyzed separately because some canopy exclosures had been established for one additional year at Austin Creek SRA, and because the species of trees used in canopy experiments were different between the two sites (mostly blue oak at Henry Coe SP, mostly black oak and live oak at Austin Creek SRA). At Austin Creek SRA in spring 2001 there were nearly three times as many seedlings in oak canopy exclosure plots (*n*=620) compared to oak canopy control plots (*n*=223). Average sizes of tree seedlings in the oak canopy exclosures at Austin Creek SRA were larger (81.1 ±1.2 mm) than in oak canopy control plots (74.6 ±2.6 mm; α=0.008). At Henry Coe SP we counted approximately similar numbers of tree seedlings in oak canopy exclosure plots (*n*=20) as in oak canopy control plots (*n*=32). Nevertheless, sizes of tree seedlings in the canopy exclosure plots (76.8 ±6.4) were larger than in the canopy control plots (60.8 ±4.2 mm; α=0.034).

Oak Acorn Survival and Oak Canopy Exclosures

Results from acorn survival monitoring during fall 1998 indicated that most acorn drop on the plots occurred from late September to mid-October. We detected fewer acorns on the control plots compared to the experimental plots on each of the four analysis dates (Paired t-test α's<0.001 for each of four comparisons). However, over 99 percent of the approximately 23,000 acorns observed on the plots in fall 1998 were either aborted or rotten. Data on acorn survival from fall 1998 are therefore of limited interest relative to potential wild pig foraging effects.

Acorn numbers were monitored in control and experimental plots beneath 15 oak trees at Henry Coe SP and 15 oak trees at Austin Creek SRA in fall 1999. Most of the acorn drop in 1999 occurred during late October and November when proportionally more of the acorns noted on the survival plots in 1999 were mature compared to 1998. At Austin Creek SRA, the total numbers of mature acorns in plots under the 15 trees ranged from 544 in September to 2,408 in mid December *(fig. 4)*. At Henry Coe SP, the total numbers of acorns in plots under the 15 trees ranged from 1892 in September to 4,960 in November *(fig. 4)*. At both Austin Creek SRA and Henry Coe SP numbers of acorns were initially higher in control plots than in experimental plots, but were less numerous in experimental plots than in control plots by midway through the monitoring period *(fig. 4)*. Analysis of data on acorn numbers beneath oak trees by repeated measures ANOVA indicated that fewer acorns survived on control plots than on experimental plots by the end of the monitoring period in mid December (α=0.001).

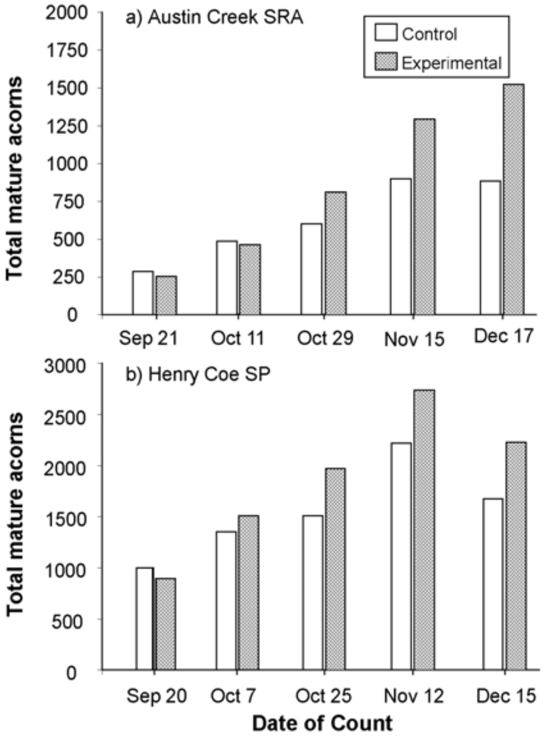

Figure 4—Results from oak canopy experiments on acorns observed on different types of monitoring plots at (a) Austin Creek SRA, and (b) Henry Coe SP during fall 1999. Data are from 16 and 15 experimental trees at Austin Creek SRA and Henry Coe SP, respectively.

Discussion

In this study we are using a combination of experimental and descriptive methods to assess multiple hypotheses related to the potential ecological effects of wild pigs on native ecosystems. After two years of research, our results indicate that rooting disturbance by wild pigs may exceed 35-65 percent annually in areas with high-density pig populations. Rooting disturbance by wild pigs contributed to significant declines in aboveground biomass productivity *(fig. 2)*, which may reduce resource availability for a wide variety of terrestrial vertebrates and invertebrates. Rooting by wild pigs was much more widespread at research sites with relatively high pig density compared to sites with relatively low pig density *(fig. 1)*. This is important because rooting disturbance may potentially alter competitive relations among plants to a greater degree in areas where pig densities are relatively high. For example, the intermediate disturbance hypothesis predicts that species diversity/community heterogeneity should be highest in areas with intermediate levels of disturbance compared to areas with very low or very high disturbance. This may be important from a historical perspective because there was another large omnivore, the grizzly bear (*Ursus arctos*), present in California until the 1920s. Historical accounts indicate that grizzly bears once consumed considerable acorn mast and “grubbed” extensively for forage in and around California’s oak woodland ecosystems (Pavlik and others 1992). The last free ranging grizzly bear in California was killed in 1922. Related to the grizzly bear's taste for acorns and grubbing behavior that may have been very similar to rooting by wild pigs (Tardiff and Stanford 1998), it has been suggested that wild pigs are the ecological equivalent of the now extinct grizzly bear in California (Work 1993). According to this hypothesis, some intermediate level of acorn foraging and rooting disturbance by wild pigs may replace the activities of grizzly bears as an important source of natural disturbance in oak woodland ecosystems. This idea remains to be quantitatively assessed.

Our data suggest that high levels of rooting by wild pigs in areas where densities exceed 2.0 pigs/km^2 is contributing significantly to reduced tree seedling regeneration in oak woodland ecosystems in California *(fig. 4)*. It was notable that most of the large seedlings encountered in oak woodlands at both Austin Creek SRA and Henry Coe SP were actually stump sprouts and not seedlings that survived from germinated acorns. Also, experimental data from both habitat plot and oak canopy exclosures at Austin Creek SRA suggest that the rooting activities of wild pigs significantly reduce tree seedling survival; the lack of differences in absolute numbers of tree seedlings in exclosure compared to control plots in habitat and oak canopy experiments at Henry Coe SP may have been due to the relatively short duration the exclosures have been present at this site. Mule deer (*Odocoileus hemionus*) also consume young oak seedlings, however, and it is possible that reduced foraging by deer in exclosure compared to control habitat plots contributed to higher seedling numbers in the exclosure woodland habitat plot at Austin Creek SRA. However, we commonly observed deer or their sign in exclosure and control habitat plots at both Austin Creek SRA and Henry Coe SP, suggesting that deer had ready access to both areas. Deer may not have had full access to all oak canopy exclosure plots, however, because these exclosures were relatively small (3x3 m) and some were situated directly beneath the canopies of oak trees.

Data on numbers of acorns associated with oak canopy experiments indicate that acorn consumption by wild pigs contributes to both reduced acorn survival to potential germination and reduced forage availability for wildlife *(fig. 4)*. Data on mature acorns from our 1999 oak canopy experiments indicated that control monitoring plots initially had higher numbers of acorns than exclosure plots in September, but that pattern was reversed by October, and progressively fewer mature acorns were located on control compared to exclosure monitoring plots from October through mid December. Rooting by wild pigs was observed within control plots on multiple occasions, suggesting that differences in acorn survival may have been due to foraging by wild pigs. As previously noted, however, it is uncertain whether deer foraged inside of all oak canopy exclosures.

Management Implications

After two years of comparative and experimental research we have been able to quantitatively assess several aspects of the rooting and foraging activities of wild pigs. Data indicate that this introduced species may be reducing tree regeneration potential and forage availability for native wildlife in California's oak woodland ecosystems. Additional longer term monitoring is underway for assessing the effects of wild pigs on plant and terrestrial vertebrate communities. The most important finding from the study to date is that wild pig rooting and foraging is significantly reducing already low levels of oak regeneration in California (McCreary 1990). Wild pigs are only one potential agent of change or disturbance impinging on oak woodlands in California, however, which continue to experience degradation by agricultural development, livestock grazing, and disease. Because it will be difficult to significantly reduce pig numbers in natural areas where hunting is prohibited, the activities of expanding wild pigs will continue to exacerbate already difficult management and conservation problems associated with California's unique oak woodland ecosystems.

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Effects of a Prescribed Fire on Oak Woodland Stand Structure[1]

Danny L. Fry[2]

Abstract

Fire damage and tree characteristics of mixed deciduous oak woodlands were recorded after a prescription burn in the summer of 1999 on Mt. Hamilton Range, Santa Clara County, California. Trees were tagged and monitored to determine the effects of fire intensity on damage, recovery and survivorship. Fire-caused mortality was low; 2-year post-burn survey indicates that only three oaks have died from the low intensity ground fire. Using ANOVA, there was an overall significant difference for percent tree crown scorched and bole char height between plots, but not between tree-size classes. Using logistic regression, tree diameter and aspect predicted crown resprouting. Crown damage was also a significant predictor of resprouting with the likelihood increasing with percent scorched. Both valley and blue oaks produced crown resprouts on trees with 100 percent of their crown scorched. Although overall tree damage was low, crown resprouts developed on 80 percent of the trees and were found as shortly as two weeks after the fire. Stand structural characteristics have not been altered substantially by the event. Long term monitoring of fire effects will provide information on what changes fire causes to stand structure, its possible usefulness as a management tool, and how it should be applied to the landscape to achieve management objectives.

Introduction

Numerous studies have focused on the effects of human land use practices on oak woodland stand structure and regeneration. Studies examining stand structure in oak woodlands have shown either persistence or strong recruitment following fire (McClaran and Bartolome 1989, Mensing 1992). Others studies show a high tolerance and survivability of trees (Griffin 1980, Haggerty 1994, Plumb and Gomez 1983), although high intensity fires can cause substantial damage and mortality to stands depending on the species (Plumb 1980, Plumb and Gomez 1983). Despite this, information on fire and maintenance of oak woodlands is deficient (Barbour 1988, Haggerty 1994). This paper reports on preliminary damage and recovery of oak trees two years after a prescribed burn.

Study Site and Methods

This study was conducted on the west-facing slopes of Poverty Ridge (37°25′N, 121°45′W, elev. 800 m.) in the Mount Hamilton area, Santa Clara County, on the northern end of the Diablo Range. Mean annual precipitation is 59 cm for this area

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[1] An abbreviated version of this paper was presented at the Fifth Symposium on Oak Woodlands: Oaks in California's Changing Landscape, October 22-25, 2001, San Diego, California.

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and was such during the two years of this study. Mean seasonal temperatures for winter and summer are 17°C and 8°C, respectively. Although the burn site is predominantly on the west side of Poverty Ridge, narrow, deeply cut drainages create a rugged terrain with steep slopes. Concomitantly, the oak woodlands vary in cover and species assemblage ranging from single black *(Quercus kellogii),* blue *(Quercus douglasii),* and valley oak *(Quercus lobata)* stands to mixed codominance. The woodlands are relatively dense, mean canopy density is approximately 50 percent, but are parceled by grassland openings across the site. Associated overstory species *Quercus agrifolia* Nee (coast live oak), *Aesculus californica* (Spach) Nutt. (Californica buckeye), *Umbellularia californica* (Hook. & Arn.) Nutt. (California bay) and *Platanus racemosa* Nutt. (western sycamore) are relatively rare and found exclusively in drainages and on mesic, north-facing slopes. The understory consists mostly of forbs and annual grasses such as *Bromus diandrus* Roth (ripgut grass), *B. hordeaceus* L. and *Avena* (oats), *Carduus pycnocephalus* L. (italian thistle), and a negligible shrub cover.

Tree diameter ranged from 3.5 cm to 137.3 cm at breast height (dbh, 1.37 m), with an average of 48.8 cm. There are very few seedlings and saplings across the site; a recent survey showed the majority of them found in blue oak dominated stands.

The three hundred acre burn was conducted on June 24, 1999, commencing on the northeastern corner of the unit near the ridge. Weather conditions at time of ignition were: 20°C, R.H. at 55 percent, and the wind was 2-4 mph from the southwest. The carrier of the fire was mostly annual grasses and forbs, typical of a fuel model 1 or 2. Fine fuel moisture estimated from weather conditions ranged from 6-8 percent. The area burned mostly under backing and flanking conditions early on and throughout most of the day. Fireline intensity was relatively low in this area as flame lengths ranged from several centimeters to 0.5 meters. Extensive black lining was established before pen flares were shot into drainages to induce spot firing. The bottom of the unit was ignited in the early afternoon where it burned under head fire conditions towards the burned areas upslope. Weather conditions during this time were 22°C, R.H. at 42 percent, and the wind was 2-4 mph out of the northwest. The drier conditions strongly influenced fireline intensity and produced brief moments of flame lengths up to 2.5 meters in height. In this area many trees were exposed to extreme heat and their crowns were completely scorched with a few incidences of leaves on lower parts of the canopy catching fire. Overall, the fire burned under conditions that kept fireline intensity fairly low and consequently limited damage to the trees; only minimal scorching on the bottom of crowns occurred with a small number of trees having 100 percent of their crown scorched. This burn could be classified as a low-to-moderate ground fire where most of the understory was consumed except for patches in drainages and on mesic slopes with dense canopies. Estimates of fireline intensity ranged from 15-750 kW/m using observations of fuel and weather conditions at the time of the fire (Rothermal 1983).

The burn area was stratified into four plots in an effort to capture the variation in fire intensity: northeast (NEAST), northwest (NWEST), southeast (SEAST) and southwest (SWEST). The NEAST plot was on the east side of the ridge near the ignition point and was the first area to burn under low intensity. The trees in this area received minimal scorching of the canopy. The NWEST and SEAST plots burned under a number of fire line conditions midday and had variable crown scorch. Lastly, the SWEST plot was the last to burn under head fire conditions and received the greatest degree of damage.

Parallel line transects were placed in each of the four plots two months after the burn (August 1999). At randomly selected points along each transect the point-centered quarter sampling method (Mueller-Dombois and Ellenberg 1974) was used to select trees for long-term monitoring of damage and recovery. In each of the four quarters, the closest oak tree was tagged and measured for diameter at breast height (dbh), height, and fire damage. Tree-damage measurements included bole-char height, presence of previous trunk scars, a visual estimation of percent of the crown scorched broken into classes, and any crown or basal resprouting. The trees did not abscise the scorched leaves following the fire, allowing for an estimate of tree damage and a 'preburn' estimate of canopy cover. A total of 208 oak trees were tagged and resampled in the summer of 2000 and 2001 for evidence of damage, recovery and survival.

Tree damage characteristics, such as amount of crown scorch and bole-char height, were tested for significant differences between plots varying in fire intensity and tree size using nonparametric ANOVA with multiple comparisons. Paired t-tests were used to tests for differences in canopy density before and after the fire within plots. Chi-square tests were used to test for differences in occurrence of fire scarring and resprouting, while binary logistic regression was used to determine the relationships between resprouting with tree size and fire damage and site characteristics such as slope, aspect, and canopy density.

A seedling survey was conducted after the burn for size, density, and resprouting. Since a pre-burn survey could not be conducted, mortality from the fire could not be determined so data will not be reported.

Results

Fire Damage

Overall, trees received minimal scorching from the fire *(table 1, fig. 1)*. Approximately 78 percent of the trees, mostly valley oaks, had less than 50 percent of their crown scorched. Of the 21 black oaks sampled, only one had greater than 50 percent of its crown scorched. Black oaks on this site are found on more mesic north facing slopes where the fire was not as intense and, consequently, received less damage. Using the Kruskal-Wallis test, mean crown scorch and mean bole char height differed significantly between plots (p=<.005 for both, *table 1*). Crown scorch on the SWEST plot was significantly higher than on all other plots, although only 18 percent of the trees had completely scorched crowns and contained the only tree that died directly from the fire. This tree was entirely burned out through the bole, probably from a preexisting scar, and fell soon after the fire. Despite this, SWEST had only a slightly higher mean bole scorch height than the lowest fire damaged NEAST plot. There was no significant difference in fire damage characteristics for tree size.

The 2-year post-burn survey revealed only two trees died during the second year after the fire, a black oak on the NWEST plot and valley oak on the SEAST plot. The black oak had a preexisting trunk scar which allowed the fire to burn out the inside of the bole, and eventually felling the weakened tree. The valley oak had a thin crown before the fire and although it resprouted from the crown and bole, it had no green foliage in the summer of 2001 and is presumed dead. Neither tree has since resprouted from the base. The deficiency of dead trees from this burn prohibited any statistical analysis on tree mortality.

Table 1—*Site and tree damage characteristics for oak woodlands two years post-prescription burn on Poverty Ridge in the Mt. Hamilton Range. Means with different letters within rows indicate significant difference by ANOVA (p<.05).*

	Low <- - - - Fire Intensity - - - -> High			
	Plot			
	N-EAST	**N-WEST**	**S-EAST**	**S-WEST**
Site characteristics				
Aspect	50°	305°	180°	238°
Slope (pct)	35	41	32	45
Canopy cover (pct)	54	36	48	41
Trees/plot (Bl-Bk-Vy)	0-2-50	29-18-17	18-0-30	20-1-23
Density (# /Ha)	32.6	67.9	73	77.5
Fire damage				
Mean crown scorch (pct)	14 **a**	26 **a**	35 **b**	50 **c**
100 pct crown scorch (n)	0	3	1	8
Mean bole char ht (cm)	6.3 **a**	24 **ab**	17 **b**	8.3 **a**
Fire effects				
Above ground mortality	0	2	1	0
Fire scars (pct)	9.1	4.2	12.5	3.9
Mean bole scar ht (cm)	2.7	0.8	5.6	3.1

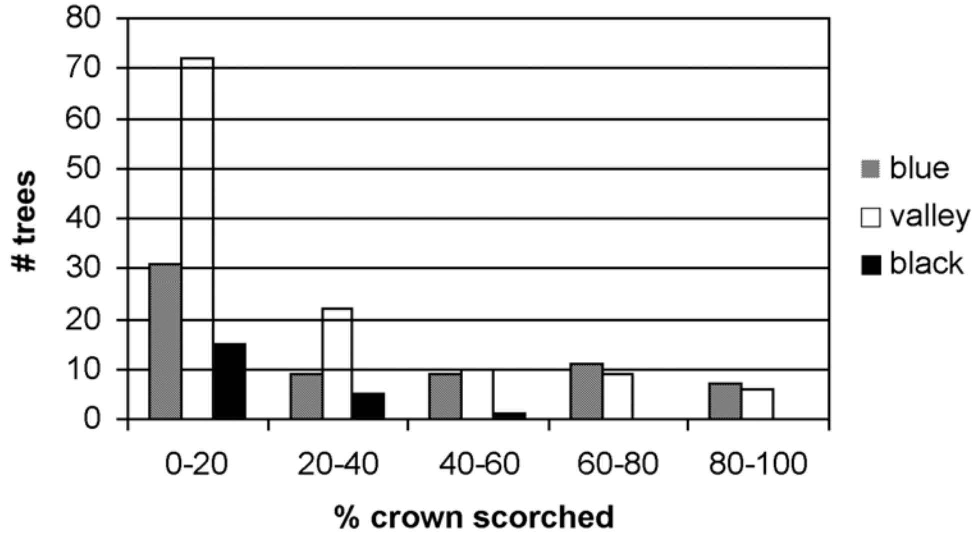

Figure 1—Amount of crown scorched, broken into size classes for three species of tagged oaks after a prescribed fire (n=208).

Recovery

Overall, percent canopy density was slightly higher for the 2001 measurements as compared to the measurements taken just after the fire in 1999 (46.67 percent and 44.14 percent, respectively). Paired t-tests showed only the SWEST and NWEST plots to be significantly different, a 7.2 percent and 5.8 percent increase two years postburn ($p<0.05$, *fig. 2*). The two other plots, SEAST and NEAST, had a less than 2 percent decrease in canopy density.

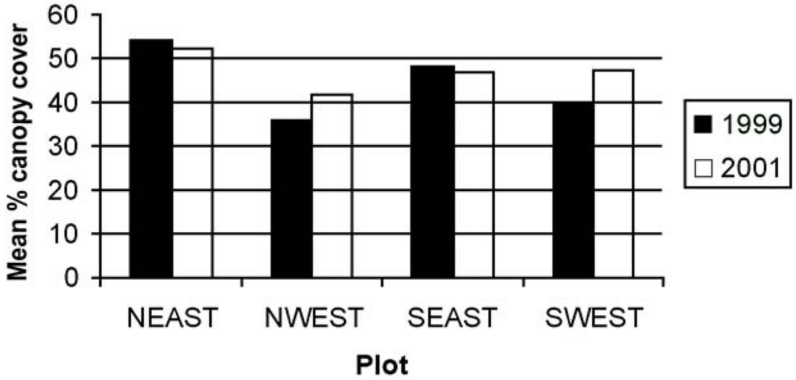

Figure 2—Comparison of average canopy cover in fire intensity plots immediately post-burn (1999) and two years post-burn (2001).

One year after the fire, crown resprouting occurred in 71.5 percent of the trees sampled, and new sprouts were seen developing on tree crowns as soon as two weeks after the fire. Less than 4 percent of the trees resprouted on the bole. Approximately 73 percent of the blue oaks and 81percent of the valley oaks that were scorched resprouted from the crown. Resprouts occurred on at least 50 percent of the trees with as low as 20 percent of their crown scorched. Chi-square tests found a significant difference in number of trees resprouting between plots (χ^2=27.6, p=.000). Only the NWEST plot had a lower number of resprouts than expected. Percent crown scorch (p=<.05) and tree size (dbh, p=.007) were significant predictors of crown resprouting using binary logistic regression analysis. Trees with higher percentage of their crowns scorched were more likely to resprout from the crown *(fig. 3)*. Resprouting also occurred on trees in all size classes. Aspect was the only environmental variable found to be significant (p=.03), with trees on southern exposures more likely to resprout.

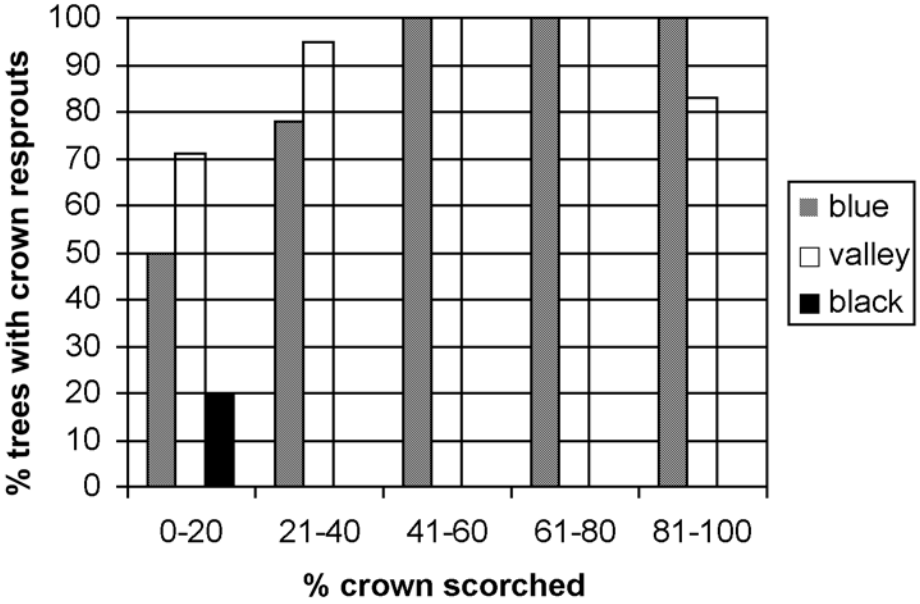

Figure 3—Tree crown resprouting as a function of crown scorched for three species of tagged oaks following a prescribed fire (n=208).

Scarring

Less than 8 percent of the trees received new trunk scars. Average scar height varied strongly between plots and occurred on just about all tree sizes. Chi-squared tests found no significant difference in occurrence of new scars between plots (χ^2=4.13, p=0.25). Old trunk scars was the only significant predictor of new scars while tree size, percent crown scorch, and site variables were not significant when analyzed by regression. Trees having old trunk scars increased the likeliness of receiving a new trunk scar and only one occurred in previously undamaged bark.

Conclusion/Discussion

The plots differing in fire intensity identified from field observations corresponded well with the degree of crown damage, but not with the occurrence of trunk scarring. Although only a small number of trees received new scars *(table 1),* this effect can cause long-term damage by predisposing trees to rot and failure, (Plumb and Gomez 1983) altering stand characteristics. Two of the three trees that died had preexisting scars which were a likely factor in their deaths. Any concern for tree survival may need to focus on factors controlling trunk scarring and not crown scorching.

Area canopy density in this study was essentially unchanged two years following the fire, being higher for only two of the four plots *(fig. 2).* Whether this was caused by fire-stimulated emergence of dormant buds, creating denser canopies, or by other variables, such as precipitation, was not investigated. However, mean annual precipitation during the two years of this study was approximate to the overall mean, although it was also about half as much as in 1998 (115 cm.).

Little change occurred in stand structural characteristics from the burn, indicating the overall low severity of the fire. Other than bole char/scars and a few clumps of dead leaves still in the canopy, most trees show no signs of the fire and have fully recovered. Species dominance was not substantially altered from this event since only three trees died, a black and two valley oaks, Although they were larger size trees (43-64 cm. dbh).

Although this is a single event, the damage, recovery, and mortality results of this study, along with previous studies (Griffin 1980, Plumb and Gomez 1983, Haggerty 1994), indicate a relative tolerance of oaks to fire. However, questions regarding the role of fire in oak woodland maintenance and recruitment still need to be investigated. It is unclear the amount of fire necessary, if at all, to sustain stands and how it influences regeneration. Overall canopy density was higher following the burn, indicating that trees had fuller, healthier crowns following the fire. Many resprouts observed from burned seedlings surveyed after the fire had greater than one shoot emerging. Increasing the numbers of shoots after a fire may increase growth rates and the chance of survival to young adults withstanding browsing pressure (Mensing 1992), competition with annuals, and subsequent fire. However, other studies suggest these factors may not play a critical role in survival (Allen-Diaz and Bartolome 1992, Sweicki and others 1990). Regeneration may be more dependent on factors controlling growth (Allen-Diaz and Bartolome 1992) such as light, temperature, and resource availability. Fire may be beneficial in creating canopy gaps allowing more light to reach the understory and creating suitable microclimate conditions for recruitment (Muick and Bartolome 1987 as referenced in Mensing 1992). A substantial increase in bare ground and percent cover of native understory plants, mostly wildflowers, was recorded following this burn as compared to the year prior (Homrighausen 2000). Studies have shown herbaceous cover, mostly grassland annuals, to increase moisture stress and deplete soil water availability, thereby adversely affecting oak seedling establishment and growth (Adams and others 1992, Gordon and Rice 1993).

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Post-fire Monitoring of Coast Live Oaks (*Quercus agrifolia*) Burned in the 1993 Old Topanga Fire[1]

Rosi Dagit[2]

Abstract

The intensity of the 1993 Old Topanga Fire raised many concerns about the recovery and response of the coast live oak trees (*Quercus agrifolia*) and their understory vegetation. Preliminary information on the status of the trees 6 months post-fire has been previously reported. This report provides follow up assessment of the condition of the 90 trees in the original study and assesses the recovery of their understory vegetation over the 8 years since the burn. This long-term study documenting the recovery of coast live oak communities in three different locations (open riparian, ridgeline and valley riparian) illustrates the recovery potential under various conditions and burn frequency histories.

Introduction

In November 1993, the Old Topanga Fire, Los Angeles County, California burned fast and furiously for 3 days under Santa Ana wind conditions, leaving behind acres of scorched hillsides and great concern about the survival rates of the affected coast live oak (*Quercus agrifolia*) trees. Initiated in January 1994, this study followed the recovery of both the oaks and their understory vegetation over time. Preliminary results were reported in Keeley and Scott (1995).

Three locations were selected for monitoring, each representing a subset of the terrain covered by oaks in the burned area. Thirty trees in Red Rock Canyon (valley riparian), Tuna Canyon (ridgeline) and Cold Creek Valley Preserve (open riparian), respectively, were selected and mapped. Selection of groves was random, based primarily on accessibility. All 90 trees experienced approximately equally high fire intensity based on the presence of white ash residue at all sites, in some places inches thick.

Summary of Site Characteristics and Fire History

Red Rock Canyon

The stream bed of this relatively steep, narrow, northeast trending canyon follows the 335 m contour as it cuts through beds of Sespe sandstones and conglomerates. Last burned in the November 1943 Woodland Hills Fire, the mature

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[1] An abbreviated version of this paper was presented at the Fifth Symposium on Oak Woodlands: Oaks in California's Changing Landscape, October 22-25, 2001, San Diego, California.

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stand of riparian oaks and sycamores was surrounded by northern mixed chaparral and grasslands with a closed canopy of up to 6 m. Dead material in the surrounding chaparral was estimated to have exceeded 50 percent (Pierpont 1994).

The oak trees line the banks of the intermittent streambed. Eleven oaks were totally burned, leaving nothing standing but charred trunks and scaffold branches. No green leaves remained on any of the trees, although some trunks were less charred.

Tuna Canyon (Bel-Mar Property)

Located on an exposed sandstone ridgeline at an elevation of 425 m, this cluster of oaks bisects the fire road and has a history of frequent fires. Part of a prescribed burn in 1988, the site was previously affected by wildfires in 1938, 1942 and 1970. The oak trees form a mature grove surrounded by annual grasses, disturbed soils and slopes covered with mixed coastal sage and chaparral. The crush and burn technique used in the prescribed burn lessened the fuel load in the area surrounding the study site, so accumulated dead material was not as abundant as that in the other two sites.

These trees received the least amount of canopy damage, but 5 oaks on the edge of the fire road, including one sapling, were completely burned. Most of the trees retained some green leaves among the crisped burned leaves.

Cold Creek Valley Preserve

The more open northeast trending riparian corridor lies at approximately the 335 m contour. The sandstone/alluvial/clay based soils support a mixed riparian community surrounded by meadows of native chaparral and introduced annuals. Last burned in the 1943 Woodland Hills Fire, the accumulation of dead chaparral material surrounding the grove was significant.

Due to the closed canopy condition at this site, there was less understory vegetation. The trees are located immediately adjacent to a perennial stream. A total of five oaks were totally burned, while the canopies of the other trees retained some green leaves amid those that burned.

Methodology

Tree conditions were observed one week following the burn in November 1993, January and April 1994, June 1996, June 1998, and June 2001. Vigor and health condition ratings were based on a system modified from the International Society of Arboriculture standard condition evaluation for landscape trees, which includes evaluation of canopy (percent cover), foliage (burned, crisped, new flush, etc.), trunk (diameter at breast height, amount bark burned, scarring, etc.), root crown condition, and overall vigor. Tree vigor was rated as dead (1) to excellent health (5). Additional notes were made concerning composition of understory vegetation, including species present and percent cover of native vs. non-native species within the driplines. Density of understory vegetation was estimated by visual review of each quadrant within the area under the canopy dripline and extending approximately 5 feet outside the edge. Trees were classed by size (range from <25 cm to >125 cm diameter at breast height). Photographs were taken from specified locations to document conditions. *(fig. 1)*

1994 **Red Rock Canyon** **2001**

1994 **Tuna Canyon** **2001**

1994 **Cold Creek Valley Preserve** **2001**

Figure 1—Photographs of burned coast live oaks in 1994 and 2001.

Results

Since initial observations were documented in January 1994, overall tree survival remains high. Of the 21 oaks severely burned in 1993, only 4 have died. All of the others have recovered. Overall survival of oaks that were severely burned at these three sites is 96 percent. Proximity to the fire front is the only common variable among dead trees.

Trunk diameter growth at the three sites is also quite remarkable, given the extent of initial canopy loss. *Table 1* summarizes the change in size class at each location. Many of the single trunk and multi-trunk trees showed consistent increase in diameter, with few remaining in the same size class since the fire. The majority of trees at all sites had recovered around 80 percent of their lost canopy by June 2001. Canopy recovery was lowest at Red Rock, where temperatures are typically colder and sunlight exposure is limited by the steep canyon walls. Canopy structure was notably normal, with predominately terminal bud flushing growth and limited epicormic sprouting. Immediately post-fire, canopy structure was more dominated by epicormic sprouting, with less terminal bud growth. Basal sprouting was minimal at all locations.

Table 1—*Size distribution of surviving oaks.*[1]

	DBH class (cm)								
Site	<25	25-50	51-75	>75	25-50	51-75	76-100	101-125	>125
1994									
Red Rock	2	11	3	1	1	2	4	3	3
Tuna Canyon	6	11	2	0	0	3	2	2	3
Cold Creek	3	1	8	2	2	1	3	2	8
Total # trees	11	23	13	3	3	6	9	7	14
2001									
Red Rock	3	7	5	1	1	1	2	4	4
Tuna Canyon	3	11	2	4	2	2	3	2	2
Cold Creek	2	3	3	5	1	0	1	4	9
Total # trees	8	21	10	10	4	3	6	10	15

[1] Some trees had multiple stems. Values listed are sums for all stems.

Using the International Society of Arboriculture (ISA) evaluation of tree condition, the vigor of the burned oaks was assessed in 1996 and again in 2001. Overall, tree condition appears to have continued improving. Few trees have declined or even remained the same *(table 2)*. (Vigor rating scale: 1=dead, 2=declining, 3=stable, 4=good, 5=excellent).

Table 2—*Average vigor of surviving oaks.*[1]

	DBH class (cm)								
Site	<25	25-50	51-75	>75	25-50	51-75	76-100	101-125	>125
1996									
Red Rock	3.5	2.5	3	4	3	3	3	3	3
Tuna Canyon	3.5	3	4	0	4	3.5	3	3	3
Cold Creek	3	3	4	3	3	2	3	3	3.5
2001									
Red Rock	4	4	3.5	4.5	5	3	3.5	3.5	4.5
Tuna Canyon	4.5	4	4.5	0	4.5	4	4	4	4
Cold Creek	3	4	4	4	4	0	3	4.5	4.5

[1] Values are based on a rating scale of 1-5, where 1=dead and 5=excellent.

Understory vegetation has remained consistent since the initial post-fire flush. During the spring of 1994, numerous "fire following" annuals sprouted along with most native species. Species like fire hearts (*Dicentra ochraleuca*), yellow fire hearts (*Dicentra chrysantha*), fire poppy *(Papaver californicum*), wind poppy (*Stylomecon heterophylla*), and large-flowered *Phacelia* (*Phacelia grandiflora*) were only seen the first spring after the fire. Over time, the "fire followers" disappeared and were replaced by more aggressive native and non-native species.

Displacement of natives by invasive exotics has occurred, primarily along the perimeter of the groves. Invasive exotics are most prevalent in Red Rock, where there is a high degree of disturbance from a trail and fire road immediately adjacent to the trees. Invasives are also quite dominant around the perimeter of the grove at Tuna Canyon, also related to high disturbance levels. The less disturbed and more closed canopy found at Cold Creek is not conducive to invasive annuals, and the dominant vegetation in the understory remains native. The most aggressive invasives are grasses (*Avena fatua, Bromus* sp., *Cynodon dactylon*, *Festuca* sp., *Hordeum murinum,* etc.) and mustard (*Brassica nigra*), followed by a variety of thistles (*Centaurea melitensis, Salsola iberica*, etc.).

The most dominant native understory plants included snowberry (*Symphoricarpos mollis*), clarkia (*Clarkia deflexa*, *C. unguiculata*), giant ryegrass (*Elymus condensatus, E. glaucus*), poison oak (*Toxicodendron diversilobum*), phacelias *(Phacelia* sp.), buckwheats (*Eriogonum* sp.), sagebrush (*Artemesia californica*), mugwort (*Artemesia douglasiana*), canyon sunflower (*Venegazia carpesioides*), and sages (*Salvia* sp.). Numerous oak seedlings were found in the understory, although few exceeded 10 cm in height. Seedling density at Cold Creek was particularly high, although recruitment of saplings (greater than 10 cm tall) has been low in general, and confined to the edges of groves where there is more light. *Table 3* summarizes the differences in understory composition between the sites. All of these sites were excluded from post-fire aerial seeding with annual ryegrass.

Table 3—*Comparison of native vs. non-native understory coverage, 2001.*

Site	Avg. pct. cover native	Avg. pct. cover non-native
Red Rock	62	38
Tuna Canyon	60	40
Cold Creek	86	14

Discussion

Post-fire survival of coast live oaks is enhanced by their thick bark and ability to regenerate lost canopy quickly following a burn (Plumb 1980). Basal sprouting was minimal (only one tree), which contrasts with results found by Pavlik (1991) and Paysen (1993). They both noted significant basal sprouting following topkill of smaller saplings and mature trees, as well as increased mortality in seedlings under 15 cm tall. Tietje and others (2001) found that topkilled coast live oak saplings consistently exhibited basal resprouting following damage in a prescribed burn. Basal sprouting was uncommon at our sites, with only one topkilled sapling responding with basal sprouts.

The majority of the oaks in the study had recovered over 80 percent canopy density within 2 years of the fire. Sprouting initially occurred both epicormically from scaffold branches and trunks, and also in a more standard pattern from terminal buds. As the years passed and the canopy spread, terminal branching took over, reducing the number of epicormic sprouts remaining. In some cases, the epicormic sprouts grew into stout branches, replacing burned scaffold branches that had fallen from the tree.

As the canopy regenerated, diameter of the trunks increased. The majority of the trees have grown substantially since the fire. Nutrient availability increases following a high intensity burn (Boerner 1988). This surge of nutrients not only supports the recovery of the trees, but also the peak of understory species richness immediately post fire. Numerous native "fire following" species were noted in the spring of 1994, followed by a decline in number of native species over the years as non-natives re-colonized. In spring 2001, species diversity is still fairly high, but reflects a higher number of invasive exotics replacing the native fire-followers. Invasive exotics were able to exploit the post-fire vegetation disturbance, resulting in higher percent cover along the perimeter of groves, especially when adjacent to continually disturbed trails and fire roads. Within the center of the oak groves, native plants are dominant.

The alteration of fire frequencies due to suppression policies over the past 100 years are considered to be responsible for the shift of landscape-level mosaics of plant communities (Callaway 1993). Low-intensity fires were a standard management tool of many California Native Americans, selecting for and encouraging growth of plants and animals needed for food, shelter and clothing. Changes in fire suppression and brush clearance policy over time has significantly altered the fuel loads, especially in chaparral–oak woodland mosaics along the urban-wildland interface (Franklin 1995).

Keeley and others (1999) compared the burn frequency and fire size in chaparral communities since 1910, finding that intervals between burns is related more to ignition sources and weather factors than to age or accumulation of fuels. Thus, Santa Ana wind conditions increase the possibility of crown fires regardless of the age of surrounding chaparral fuels, and are significantly more damaging to the trees than a cooler, non-wind driven understory burn. In the Santa Ana driven 1993 Old Topanga Fire, crown fires did occur at the Red Rock and Cold Creek sites, both of which also had 50 years of accumulated dead fuels in the surrounding chaparral and understory communities. Charred skeletons were all that remained of several trees in each location. Due to a prescribed burn following brush crushing at the Tuna Canyon site, overall fuel loads were reduced adjacent to the trees. Even though the flame lengths were significantly greater as the fire rushed up the slope, fewer trees were completely burned and canopy damage was less immediately following the fire. This finding appears consistent with the recommendation of Keeley and others (1999) to focus intensive management at strategic locations along the urban-wildland interface, rather than attempt large scale fuel modification. This strategy would limit the extent of ecological disturbance conducive to the spread of invasive exotics, while still providing necessary protection to structures and significant oak stands located at the interface zone.

Summary

Post-fire recovery of coast live oaks burned in the 1993 Old Topanga Fire was excellent, with 96 percent of the trees surviving after 8 years, most with over 80 percent canopy cover. The age of the surrounding chaparral vegetation influenced the extent of crown fires, but not overall tree survival. Canopy recovery initially was dominated by epicormic sprouts from the scaffold branches, giving way over time to a more normal pattern of terminal bud growth. Fear of excessive tree mortality due to high understory fuel loads was unfounded. Tree mortality was related more to location in relation to fire intensity and flame length, than to size. Basal sprouting was minimal, with canopy recovery generated instead from charred scaffold branches and terminal buds. Immediate post-fire understory diversity was high due to the appearance of "fire following" annuals. Percent cover of natives is higher than non-natives at all sites, but due to the invasion of exotic weeds, species diversity remains higher in the more disturbed locations along the edges of groves than in the native dominated understory of the closed oak canopy. Oaks thus demonstrated once again their ability to withstand the assault of wind driven wildfires.

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Effects of Fire on Naturally Occurring Blue Oak (*Quercus douglasii*) Saplings[1]

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Abstract

We studied the survival and regrowth of naturally-occurring blue oak saplings burned in a September 1996 arson fire in Vacaville, California. The saplings (pre-fire height 33-353 cm) were burned in a rapid, low-moderate intensity fire. Of 67 blue oak saplings surveyed, 4 failed to resprout after the fire and 2 more died within the following 5 years (9 percent mortality overall); all mortality was among saplings less than 100 cm tall. Saplings which were completely topkilled (51/67) were significantly smaller on average than those which were only partially topkilled (12/67). Saplings taller than 201 cm or with a stem diameter greater than 5.6 cm at 30 cm height were only partially topkilled. Only 20 percent of the completely topkilled saplings had regained both their post-fire height and diameter by 5 years after the fire. Height growth of new shoots from completely topkilled saplings was highest in the first year after the fire, but declined in succeeding years. High levels of vole damage in resprouted topkilled saplings has adversely affected growth and shoot survival. Our observations indicate that fire negatively impacts small blue oak saplings and does not favor blue oak regeneration, as has been suggested by other authors.

Introduction

Fire plays an important role in the maintenance of numerous plant communities in California but little is known about the role of fire in the sustainable management of California oak woodlands. Several lines of evidence have suggested that fire is necessary to prevent areas with black oak (*Q. kelloggii*) and Oregon oak (*Q. garryana*) from being invaded by conifers (Fritzke 1997, Hastings and others 1997). Change in fire frequency has been suggested as a reason for the failure of oak regeneration in many areas (Pavlik and others 1991), but there is no direct evidence indicating that fire actually aids regeneration of blue oak (*Quercus douglasii*).

In a previous study on blue oak sapling recruitment in 15 locations, we found that sapling recruitment was not dependent upon fire and that repeated fires reduced sapling populations (Swiecki and others 1997). Similarly, Roy and Vankat (1999) found no blue oak regeneration when they resurveyed plots in Sequoia National Park, some of which had burned. Mortality of mature trees was greater in burned plots, but the paper does not report whether the differences were statistically significant. Employing dendrochronlogical methods to age trees and fires, Mensing (1992) and McClaren and Bartolome (1989) showed an association between blue oak stem age

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and fire occurrence. Some authors (McClaren and Bartolome 1989, Mensing 1990, Pavlik and others 1991) have suggested that this association supports the hypothesis that fire promotes blue oak regeneration, perhaps by accelerating growth rates of post-fire shoots and suppressing competitive weedy vegetation.

An alternative explanation of the historical association between fire and blue oak regeneration is that fire destroys the tops of young, pre-existing blue oaks which resprout after the fire. Under this hypothesis, cohorts of new sprout-origin trees would all date to the time of the fire occurrence. Because this recruitment is the direct result of fire-induced topkill of existing oaks, fire does not cause a net increase in the oak population and thus has no positive effect on regeneration.

In this study, we observed the fate and regrowth of naturally-occurring blue oak saplings burned during an arson fire in Vacaville, California. The objectives of this study were to document the sensitivity of small blue oak saplings to topkill by fire and to determine the length of time required for new shoot growth to replace shoots destroyed by fire. Partial results of this study have been reported (Swiecki and Bernhardt 1999).

Methods

The study site is on City of Vacaville open space lands located south of Interstate 80 on the northeast end of Lagoon Valley. The hillside supports a mixed oak woodland dominated by blue oak, valley oak (*Q. lobata*), interior live oak (*Q. wislizeni*), and California buckeye (*Aesculus californica*). The woodland, some of which was previously cultivated as orchards, contains a number of large old clearings. Vegetation in the clearings consists mostly of nonnative annual grasses and weedy forbs, but we had observed relatively high numbers of small blue oak seedlings and saplings along the edges of clearings. The complete grazing history of the study site is not known. The area was not grazed during the study and has not been grazed at least for 10 years prior to the study.

In late September 1996, an arson fire burned much of the open grassland areas and partway into the understory of the adjacent oak woodland. Fire fuels in the openings where the blue oak saplings were located consisted primarily of dry annual grasses and forbs, which were completely consumed in the rapid, low-moderate intensity fire. No mature trees were killed by the fire although a few mature interior live oak trees (*Q. wislizeni*) in the burned area developed moderate to severe trunk scarring after the fire.

Due to characteristics of the fire, the small blue oak saplings at the site were heat-killed but not consumed by fire. We were therefore able to locate and measure the height and diameter of the heat-killed stems, which were still standing and intact at the time of our initial survey (June 2-5, 1997). At that time, we located and tagged 67 blue oaks saplings located in several groupings in the burned area. We recorded the post-fire status of each sapling (partially topkilled, completely topkilled with live basal sprouts, or dead).

For completely topkilled saplings, we measured the height of the tallest heat-killed stem, as well as the diameter at ground level and at 30 cm (D30) of the largest stem. Due to dehydration of killed stems prior to initial measurements in June 1997, these pre-fire stem diameters are likely to be somewhat smaller than actual pre-fire diameters of live stems. We also counted the number of heat killed and live shoots and the height of the tallest live shoot. Because these sprouts were very thin (generally 0.5 cm or less) we did not attempt to measure their diameters in the first post-fire survey.

For partially topkilled saplings we recorded the height of the tallest branch prior to the fire. This was the greater of the tallest dead shoot or the height to the previous season's live shoot tip (based on the location of terminal bud scars). We measured the height of the tallest currently live stem, and stem diameters at ground level, 30 cm, and 137 cm diameter at breast height (DBH) if applicable. We also visually estimated the percent of the canopy which had been heat-killed.

Tagged saplings were relocated and reevaluated annually through July 2001. Annual measurements were made in midsummer or later, after the current season's shoot was largely complete. Because basal diameter and D30 measurements were highly correlated and D30 measurements were much easier to make, we only measured D30 and DBH for the largest stem of each saplings after 1997. Only D30 stem diameters are reported in this paper. We also measured the height of the tallest shoot, the number of stems, and rated the presence and severity of meadow vole (*Microtus californicus*) damage in the annual evaluations. Data for one to two saplings are missing in certain years because they were not located during the survey.

We used JMP statistical software (SAS Inc., Cary NC)[3] for data analysis. Unless otherwise indicated, effects or differences are referred to as significant if $P \leq 0.05$. We used logistic regression models to examine the effects of plant factors on the binary outcome total or partial topkill. We used paired t tests to compare heights of saplings made in different years. Because delayed topkill and mortality occurring during the study caused annual changes in the number of trees in each status category, the sapling counts are presented along with percentages if based on a total other than all 67 tagged saplings.

Results

Effects of Fire on Plant and Shoot Survival

Of the 67 saplings included in the study, 12 (18 percent) were only partially topkilled as of June 1997. In June 1997, levels of crown damage in partially topkilled saplings ranged from less than 2.5 percent to over 80 percent crown dieback. Two saplings that showed only partial topkill in June 1997 died back to root sprouts between June 1997 and October 1999; both of these saplings had more than 50 percent crown dieback in June 1997. These saplings are included in totals for completely topkilled saplings in the data for 1999 onward.

The fire caused complete topkill of aboveground shoots in 55 (82 percent) of the saplings. Four topkilled oaks (6 percent) failed to resprout and were dead as of June 1997. In addition, 2 oaks that had resprouted from topkilled saplings died between the 1999 and 2001 evaluations. Hence, by 5 growing seasons after the fire, overall mortality was 9 percent (6/67) and 84 percent (51/61) of the surviving oaks were represented by resprouts whose shoots originated after the fire.

Pre-fire heights of saplings from the burned area ranged from 33 to 353 cm. Of the saplings that were shorter than 150 cm, 98 percent (51/52) were completely

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[3] Mention of trade names or products is for information only and does not imply endorsement by the U.S. Department of Agriculture.

topkilled; this includes all 4 of the topkilled saplings that failed to resprout. In contrast, only 27 percent (4/15) of the saplings that were at least 150 cm tall were topkilled and no sapling taller than 201 cm was completely topkilled. Although we do not have the exact pre-fire stem diameter of the saplings, stem diameters measured in June 1997 show a similar threshold effect for sensitivity to topkill. Only 4 percent (2/55) of completely topkilled stems measured in 1997 were thicker than 4 cm D30. No sapling greater than 5.6 cm D30 in 1997 was completely topkilled, but some saplings with stems as small as 1.7 cm D30 were only partially topkilled. Both sapling height and stem diameter were highly significant ($P<0.0001$) predictors of complete topkill in univariate logistic regression models.

Post-fire Regrowth

Prior to the fire, most saplings (52 percent) had only a single stem at ground level. Among the saplings that were completely topkilled by the fire and resprouted, 57 percent (29/50; data for 1 sapling missing) had a single stem and only one (2 percent) had five stems. In the second year after the fire (1998), only 10 percent (5/50) of the completely topkilled saplings had a single stem and 86 percent (43/50) had 5 or more stems. Due to damage by voles and other factors, the number of stems among the completely topkilled plants has declined over time. By July 2001, only 61 percent (30/49) of the surviving completely topkilled oaks had 5 or more stems. The situation for the partially topkilled saplings was somewhat different. By 1998, fire had reduced the stem number of three of the partially topkilled saplings by destroying small suppressed stems and basal sprouts. The remaining trees either showed no change in stem count (5/12) or an increase in stem count due to damage-induced stimulation of new basal sprouts. Because most of the new or lost stems in the partially topkilled saplings were much smaller than the main stem, the overall form of these saplings was not affected substantially by the fire.

New shoots produced by completely topkilled saplings grew most rapidly in the first season after the fire *(fig. 1)*. Height growth slowed considerably after this initial growth spurt. This is due in part to the fact that most resprouted saplings were multistemmed and in part due to the loss of dominant stems after 1998 as the result of vole damage. By five years after the fire (2001), 27 percent (14/51) of the surviving topkilled saplings had regained their pre-fire heights. However, surviving completely topkilled saplings were still significantly shorter overall in 2001 than they were pre-fire (paired t test $P<0.0001$).

Average stem diameters of completely topkilled saplings decreased significantly after the fire because new shoots were much narrower than the original heat-killed stems *(fig. 2)*. Five years after the fire, stem diameters of the resprouting shoots were still significantly less than those of the pre-fire saplings (paired t test $P<0.0001$). Only 25 percent (13/51) of the surviving topkilled saplings have diameters equal to or greater than those measured in June 1997.

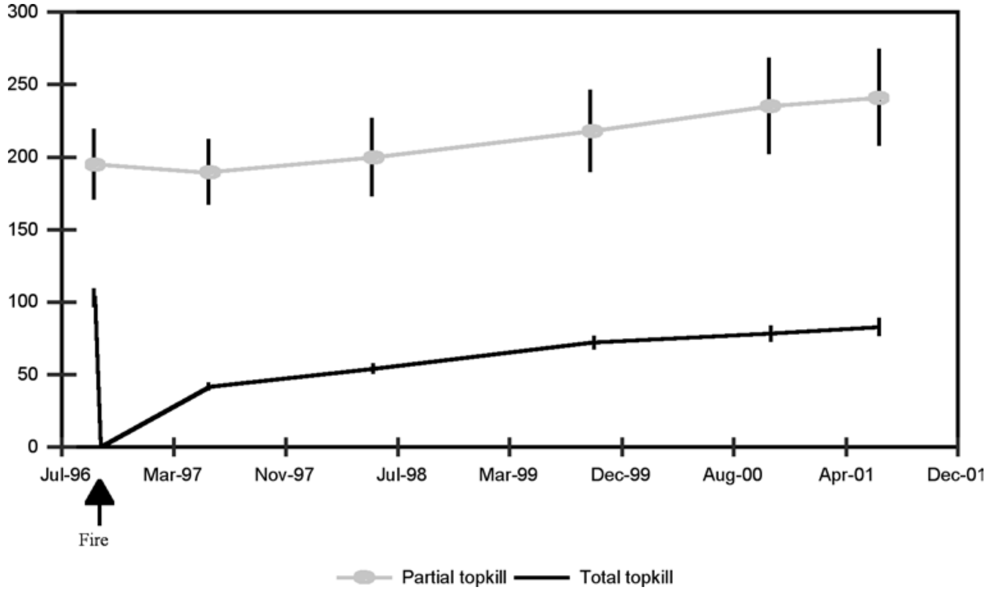

Figure 1—Average heights over time of saplings initially partially or completely topkilled by fire. Graph excludes heights of two saplings initially rated as partially topkilled that later died back to root sprouts. Vertical bars at each data point represent standard error, note that error bars for total topkill data points are mostly smaller than the rectangular markers.

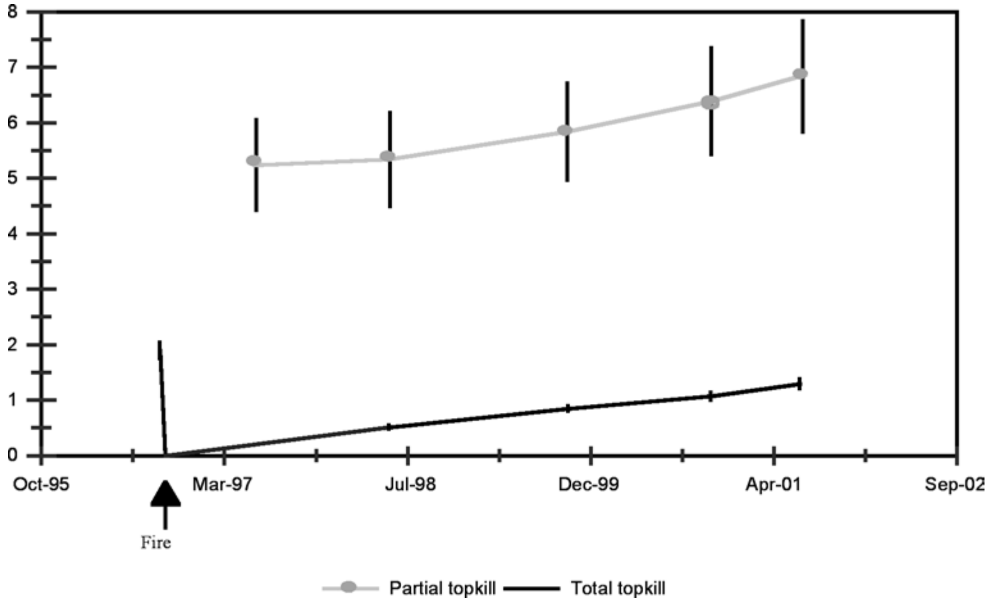

Figure 2—Average stem diameters at 30 cm of saplings initially partially or completely topkilled by fire. Graph excludes diameters of two saplings initially rated as partially topkilled that later died back to root sprouts. Vertical bars at each data point represent standard error, note that error bars for total topkill data points are mostly smaller than the rectangular markers.

If pre-fire height and stem diameter in June 1997 are used jointly to determine that a sapling has gained parity with its pre-fire condition, only 20 percent (10/51) of the completely topkilled saplings had reached parity within 5 years after the fire *(fig. 3)*. June 1997 stem diameters of the saplings that achieved parity within 5 years were all less than 3 cm. Only one sapling that achieved pre-fire parity within 5 years was taller than 100 cm *(fig. 3)*.

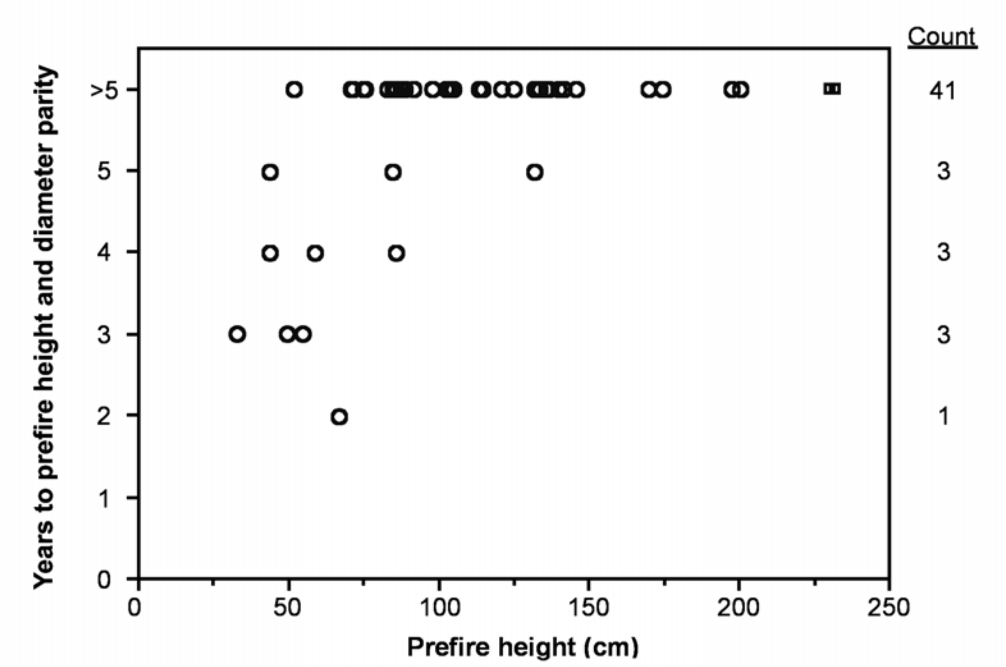

Figure 3—Years required for completely topkilled saplings to regain both pre-fire height and diameter at 30 cm as a function of pre-fire height. Square symbols represent two saplings originally classified as partially topkilled that died back to the ground after June 1997.

With the exception of two saplings which eventually died back to root sprouts, saplings with only partial topkill recovered within about 2 years from the effects of the fire *(figs. 1 and 2)*. Annual rates of diameter and height growth were comparable to those of two unburned saplings from the same area (data not shown). Partially topkilled saplings showed significant increases in both height and stem diameter between 1997 and 2001 (paired t tests, $P=0.0052$ and $P<0.0001$, respectively). These analyses do not include the two partially topkilled saplings that later died back to the root crown.

In the October 1999 survey, we observed substantial amounts of vole damage on both study saplings and other woody vegetation in the study area. Due to their smaller stem diameters, the completely topkilled saplings experienced both higher rates of damage and greater damage severity than the partially topkilled saplings *(table 1)*. Besides contributing to the reduction in shoots per plant as noted above, vole damage sometimes eliminated the tallest shoot, resulting in losses in height *(table 1)*. Vole damage apparently contributed to the demise of the two topkilled saplings that died after 1999. Although deer are present in the area, damage due to deer browsing was not appreciable over the course of the study.

Table 1—*Current-season vole damage and losses in stem height observed in the 1999 through 2001 evaluations.*

Variable	Sapling class	Evaluation date Oct 1999	 Nov 2000	 July 2001
Saplings with current season vole damage	Partially topkilled	20 pct (2/10)	40 pct (4/10)	10 pct (1/10)
	Completely topkilled	68 pct (36/53)	83 pct (43/52)	39 pct (20/51)
Saplings with height reductions relative to the previous year	Partially topkilled	10 pct (1/10)	0 pct (0/10)	10 pct (1/10)
	Completely topkilled	13 pct (7/53)	23 pct (12/52)	22 pct (11/51)

Discussion

Our observations at this site provide no support for the hypothesis (McClaran and Bartolome 1989, Mensing 1990, Pavlik and others 1991) that fire promotes blue oak regeneration. Rather, it is apparent that even in a fairly mesic site, fire damage retards the advancement of small saplings to the overstory. Although resprouting topkilled saplings may show high rates of height growth immediately after a fire *(fig. 1)*, fast growth rates are not sustained over time. Many years are required for topkilled saplings to simply regain the aboveground biomass that they possessed before being burned *(fig. 3)*. During this period of regrowth, saplings remain highly vulnerable to damaging agents including voles, browsing vertebrates, and additional fires. Furthermore, the regrowth of preexisting saplings cannot be interpreted as net regeneration. When mortality due to fire and other post-fire factors are considered, it is clear that fire negatively affects tree recruitment from small saplings.

Similar conclusions were drawn by Allen-Diaz and others (1990) who reported on a small study involving blue oak saplings between 50 and 70 cm tall. In that 3-year study, which included only 24 burned and 24 nonburned saplings, the authors concluded that fire set back the growth of small shrubby blue oaks and did not stimulate regeneration or regrowth. Associations between estimated fire history and blue oak regeneration drawn from dendrochronological studies (McClaren and Bartolome 1989, Mensing 1992) result because fire temporally concentrates shoot ages of sprouts through topkill. Although other studies that report on direct effects of fire on blue oak have involved either larger (Haggerty 1994, Roy and Vankat 1999) or smaller (Allen-Diaz and Bartolome 1992, Schwan and others 1997) oaks than those in our study, none of these studies provide evidence that fire favors blue oak regeneration.

The threshold for initial complete topkill in this study was about 1.5 m to 2 m height or about 4 cm to 5.5 cm diameter at 30 cm. Data from more fires of varying intensities would be needed to determine whether sapling height or diameter is a better predictor of complete topkill across a range of fire characteristics. Knowledge of the size threshold for sapling topkill has important implications for the use of fire in blue oak woodland management. Land managers might avoid the use of fire or otherwise protect saplings below the threshold size if recruitment of such saplings to the tree stage is a management goal. Furthermore, when combined with site-specific growth data, the threshold size could be used to determine the minimum fire interval needed to permit trees to be recruited from sprouts of topkilled saplings. After 5 years, none of the completely topkilled saplings at this site have grown large enough to survive another fire equivalent to the 1996 burn. Even at this relatively favorable site, it seems likely that many saplings will not grow beyond the topkill threshold for at least another decade. At a site where height growth is limited by livestock or deer browsing, repeated fires may serve to eliminate regeneration (Swiecki and others 1997).

The number of unburned saplings in the study area was insufficient to allow for the monitoring of a control population, but our observations of unburned saplings in and near the study area suggest that these were at no disadvantage relative to their topkilled counterparts. Many small, nonburned saplings, and even some small trees were damaged in the vole outbreak years. However, these saplings have had to contend with only a single round of shoot loss or damage over the past 5 years, compared with the two shoot loss events experienced by topkilled saplings that were later attacked by voles. Repeated shoot loss increases the mortality rate of small blue oak seedlings (Swiecki and others 1991). Although blue oak saplings have adaptations that allow them to withstand occasional shoot loss, repeated shoot damage or loss caused by fire or other agents suppresses sapling growth and results in increased sapling mortality.

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Effects of Wildfire on Blue Oak in the Northern Sacramento Valley[1]

Marc Horney,[2] Richard B. Standiford,[3] Douglas McCreary,[4] Jerry Tecklin,[4] and Roy Richards[5]

Abstract

The objective of this project was to develop a technique for rapidly determining the extent of wildfire damage to blue oaks (*Quercus douglasii*) that would be usable by landowners without requiring extensive training. In late winter 2000, 100 oaks of various sizes and degrees of damage were selected from 10 plots located where wildfires had burned in the previous year. Measures of individual tree parameters, stand structure and scorch characteristics were taken and tested for their adequacy in predicting mortality. These same oaks were re-evaluated in August 2000. Sixteen percent of the sample trees were top-killed (50 percent of the seedlings, and 8 percent of the saplings and mature trees). Eighty-eight percent of the top-killed oaks re-sprouted from the base. Only two of the top-killed oaks in this study failed to re-sprout. Logistic regression models based on tree size and wildfire effects are presented as preliminary tools to predict wildfire effects. The low level of mortality confirms the tolerance of blue oak to low- to moderate-intensity wildfires.

Introduction

Because the major oak woodland species have not been considered commercially important in California, only relatively recently has there been much demand for information on the effects of fire on mortality and recruitment. As a consequence, the impacts of fire on these hardwood species are not entirely understood.

Although oaks are generally resistant to damage by fire (Mooney 1977, Plumb and Gonzalez 1983), accumulations of fine fuels, combustible debris and increasing densities of shrub species that can convey fire into oak canopies may create fire conditions that may result in catastrophic damage to trees in oak woodlands (Mensing 1992). These hazardous conditions appear to have become more prevalent over the last 60-70 years as a result of increased fire suppression efforts (McClaran

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[1] An abbreviated version of this paper was presented at the Fifth Symposium on Oak Woodlands: Oaks in California's Changing Landscape, October 22-25, 2001, San Diego, California.

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and Bartolome 1989). In the aftermath of fires, landowners and managers may desire to identify trees that have been severely injured in order to estimate losses to property values and to plan restoration efforts. A method for rapidly assessing the severity of burn damage to affected oaks would be useful for restoration projects and for the management and monitoring of prescribed burns.

This research project was designed to develop a method for evaluating fire-damaged oaks that private landowners and forestry professionals alike can use for rapidly estimating mortality in various size classes of blue oaks. In the process we expected to add to the body of knowledge about fire ecology in oak woodlands.

Methods

Four study sites were selected in blue oak woodlands that were burned by wildfires in the summer of 1999 at the north end of the Sacramento Valley in eastern Tehama County. Descriptive measures of tree characteristics (diameter breast-height, total height, crown height and width, height base to live crown and bark thickness), stand structure (basal area, canopy cover, presence of ladder fuels) and scorch characteristics (percent bole charred, height of bole char, bole char severity, bud damage and percent crown scorch) were recorded for each of the trees in winter 2000. In August 2000 height base to live crown, presence of acorns, vigor (Dead, Low, Moderate, Good) and sprouting (Absent, Weak, Vigorous) were evaluated for these same trees. Fire effects were evaluated by the height of crown foliage scorch, the percentage of the live crown affected, and the amount of bud damage. The charring on the bark was evaluated as a proxy for the heat reaching the cambium. Components of bark charring included height of char, the amount of bark consumed and the percent circumference of the bole charred. Bud damage was categorized as "all dead," "some live," or "most/all live."

Mortality data were analyzed using two sample t-tests and a maximum likelihood estimation procedure. Using the t-test approach, trees were tested as two classes: live (those with intact above-ground tissues remaining) and dead (those that had been top-killed and may or may not have re-sprouted the following spring).

The hypothesis was that the probability of survival the following growing season was a function of tree size and condition (height, diameter breast-height, crown width, crown length, bark thickness), apparent fire effects (percent crown scorch, bud damage, bole char), and adjacent vegetation (basal area of competition, presence of ladder fuels). The predicted value of the dependent variable, LIVE, can be interpreted as the probability of a particular tree surviving the fire.

LIVE = f(tree size and condition, fire effects, adjacent vegetation).

Since the dependent variable, LIVE, is a discontinuous variable having a value of 0 (tree died) or 1 (tree survived), logistic regression procedures were used to develop the statistical model. This process transforms the dependent variable using the logistic function, and estimates the coefficients for the independent variables shown in the general equation below using a maximum likelihood estimation process (Wonnacott and Wonnacott 1979).

$$\text{LIVE} = \frac{1}{1 + e^{-(x'\beta)}}$$

Where: LIVE = dependent variable (1 = tree survived, 0 = tree top-killed)

x = vector of independent variables

β = = logistic regression coefficients

Results

In the August 2000 assessment, 16 percent of the trees had been top-killed. Of these, however, only two had failed to re-sprout. A summary of t-test results for variables significantly associated with top-kill are given in *table 1.*

The results of the maximum likelihood estimation procedure for seedlings (less than 3 feet tall) and saplings (trees 3 to 10 feet tall) are shown below in *table 2.* The results of tree survival (trees > 10 feet tall) are shown below in *table 3.* Because these variables explain between 86 percent and 96 percent of the variation in mortality, we believe they represent an adequate prediction set for identifying trees that have a high likelihood of succumbing to fire effects.

Table 1— *T-test results for parameters significant at P<.01.*

Variable	Class means	
	Live	**Dead**
Bole char severity	2.5	1.3
Crown diameter (ft.)	13.0	5.6
Diameter (cm)	7.6	2.1
Tree height (ft.)	20.4	10.3
Bark thickness (cm)	0.49	0.11
Percent scorch	66	98
Bole char (pct)	31	74

Table 2—*Logistic analysis of blue oak seedling and sapling survival (under 10 feet tall) following wildfire.*[1]

Variable	Coefficient (significance)
Constant	-5.2002 (**)
BA = Stand basal area in square feet per acre	0.07607 (*)
HT = total tree height (feet)	0.68888 (**)
CHARHT = height on bole with blackened char (feet)	-2.9331 (**)
CHARSEV = char severity rating (1 = completely black, bark reduction; 2 = black into crevices, no bark reduction; 3 = black on surface, not inner crevices; 4 = no char)	2.5328 (**)
Equation significance	(**)
Percent of variability in survival explained by model	0.86

[1] Significance with one (*) indicates variable was significant at p=.05. Two (**) indicate variable was significant at p=.01

Equation (1) shows the blue oak seedling and sapling survival equation developed from the transformed logistic regression (see *table 2* for a description of variables). A similar transformation is made to develop the blue oak tree survival model from the results shown in *table 3.*

$$(1)\ \mathrm{LIVE}= \frac{1}{1+e^{-(-5.2002+0.07607\times \mathrm{B}A+0.68888\times \mathrm{HT}-2.9331\times \mathrm{CHARHT}+2.5328\times \mathrm{CHARSEV})}}$$

Table 3—*Logistical analysis of blue oak survival (> 10 feet tall) following wildfire.*[1]

Variable	Coefficient (significance)
Constant	-1.1703
DBH = Diameter at breast height (inches)	0.83702 (**)
CHARPCT = percent of bole circumference with char at 1 foot	-6.4627 (**)
CHARSEV = char severity rating (1 = completely black, bark reduction; 2 = black into crevices, no bark reduction; 3 = black on surface, not inner crevices; 4 = no char)	2.1847 (**)
Equation significance	(**)
Percent of variability in survival explained by model	0.96

[1] Significance with one (*) indicate variable was significant at p=.05. Two (**) indicate variable was significant at p=.01

Discussion

The severity of damage from fire is largely dependent on the temperature reaching the living cells of the cambium beneath the bark (Plumb and Gomez 1983). Owing to their greater thickness of protective bark, larger trees are much more resistant to high temperature fires than small trees. Fire can also seriously damage trees when it reaches the crown. Taller trees with elevated crowns are more immune to crown fires than shorter trees, but ladder fuels can make all tree classes vulnerable and high tree densities can lead to the spreading of crown fires once they occur. In the case of the trees we examined, blue oaks proved highly resistant to top-kill from fire except for those in the smallest size classes and those individuals that were in close proximity to ladder fuels that carried fire into the crown and fallen debris that burned at high temperature in close physical proximity to the bole. We noted that damage to oaks was relatively minor in areas where fine fuels had been reduced by grazing prior to the fire. *Figures 1-4* illustrate how tree survival changes with tree size, char height and char severity. The three lines in each graph represent the three char severity ratings (CHAR 1 is most severe, CHAR 3 is least severe—see *table 2* for description of char variable). *Figures 1 and 2* present the data for seedlings and saplings grouped within two char height classes, representing tree size in terms of total height. Figures 3 and 4 present the data for older trees grouped within two bole diameter classes, representing fire effects in terms of percent bole char.

These analyses indicate that a 4-point bole char severity rating plus char height and total tree height (young oaks) or percent bole charred at 1 foot and bole diameter (older trees) provided good prediction of mortality. The bole char severity rating procedure can easily be taught to general audiences and the remaining three measurements are likewise straightforward and require no special training or tools.

We therefore believe that we have the basis for a useful tool that we can provide to all groups interested in oak fire assessment.

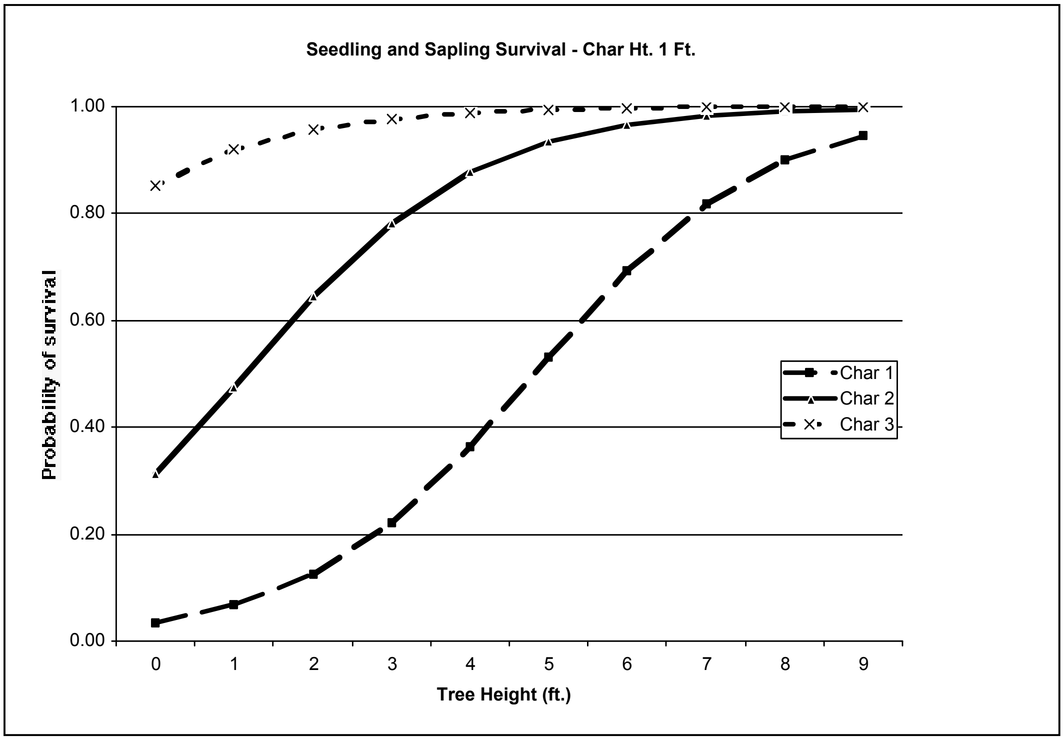

Figure 1—Seedling and sapling survival, char height 1 foot.

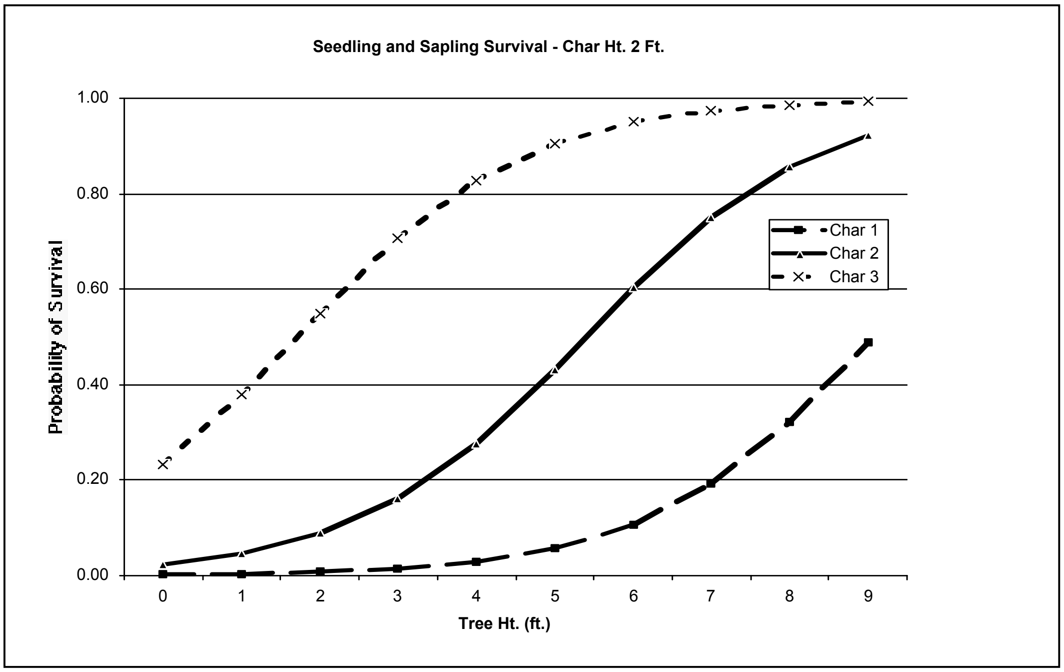

Figure 2—Seedling and sapling survival, char height 2 feet.

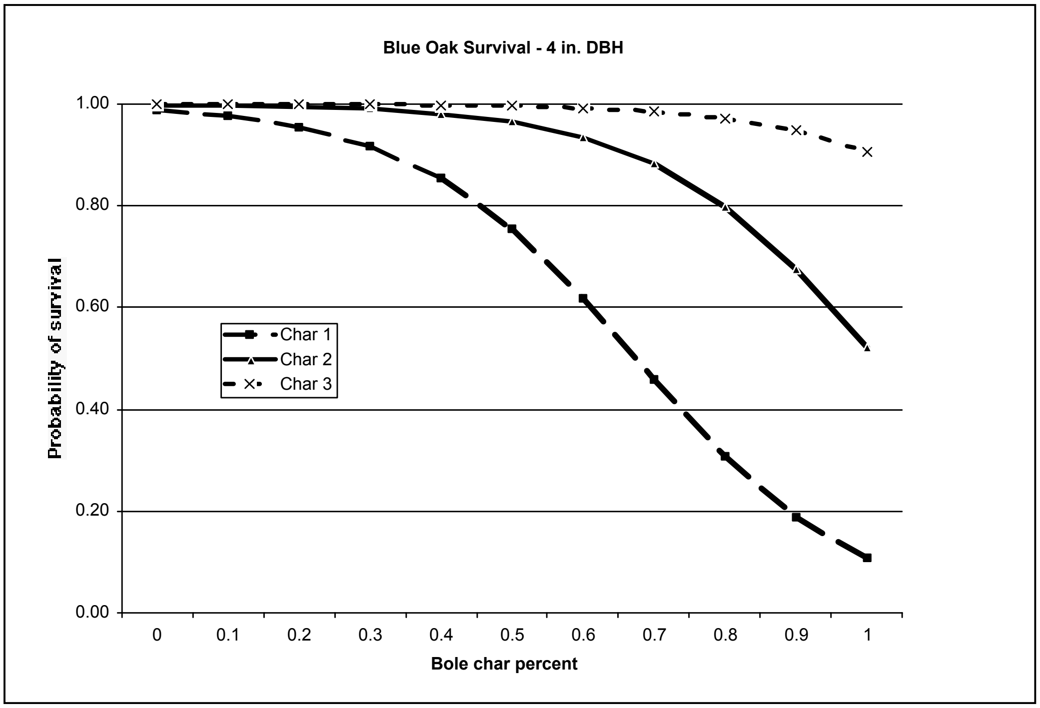

Figure 3—Tree survival, DBH 4 in.

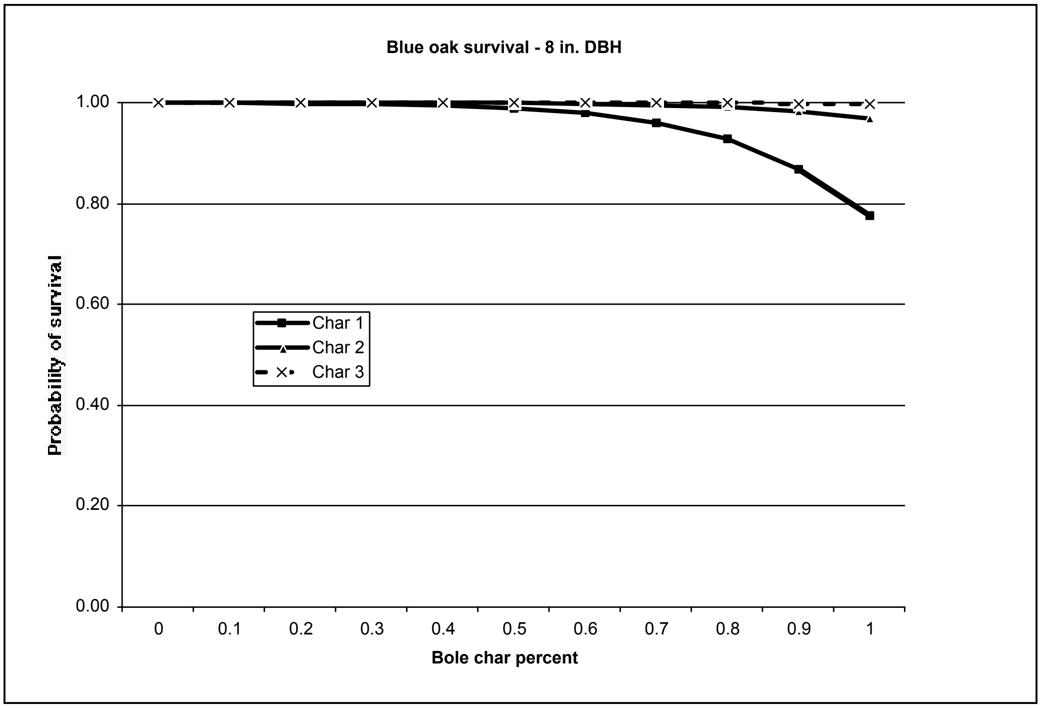

Figure 4—Tree survival, DBH 8 in.

Conclusions

The techniques applied in this study have produced procedures that correctly predict the likelihood of top-kill in blue oak stands following fire for over 85 percent of the trees analyzed. The parameters used in the model are straightforward enough to be used by landowners and other non-professionals after minimal training. Further refinements to these models following more extensive applications may produce some improvement in accuracy, usefulness and scope.

In terms of mortality effects, it seems that size is an indication of the likelihood of trees dying from the fire as several different variables that were related to size were significantly different for alive and dead trees with small trees more likely to be killed (diameter, height, bark thickness, crown diameter).

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Numerical Response of Small Vertebrates to Prescribed Fire in a California Oak Woodland[1]

Justin K. Vreeland[2] and William D. Tietje[3]

Abstract

Use of prescribed fire for management of livestock forage and fuel load is increasing in California oak woodlands, but its effects on vertebrate wildlife are unknown. We conducted a light-intensity prescribed fire in mixed blue oak-coast live-oak woodlands in coastal-central California and assessed vegetation change and numerical response of small, non-game vertebrates, to the fire. The prescribed fire significantly reduced four (grass, shrub cover, coarse woody debris, woodrat houses; $P<0.05$) of the 13 vegetation and habitat components that we measured. We observed no change in relative abundance of small mammals, breeding birds, amphibians, or reptiles in response to the prescribed fire. Light- to moderate-intensity prescribed fire in California oak woodlands is probably beneficial by reducing resource competition from exotic annual grasses, stimulating shrub and tree vigor and, ultimately, overall habitat rejuvenation. A high-intensity prescribed fire is planned for the fall of 2002 to yield a better understanding of the response of terrestrial vertebrates to the range of prescribed fires that are conducted in California oak woodland.

Introduction

Oak (*Quercus* spp.) woodlands are the most extensive vegetation type in California, covering approximately 3 million ha (Griffin and Muick 1984, Rossi 1979). In varying compositions, 10 native shrub and nine native tree species comprise numerous woodland habitat types. More vertebrate wildlife species use oak woodlands than any other vegetation type in California (Airola 1988, Ohmann and Mayer 1987).

California oak woodlands are fire-adapted, having evolved with fire during the past one million years. The dominant use of oak woodlands is rangeland for livestock production. Prescribed fire is used in oak woodlands as a livestock forage and fuel management tool (Griffin and Muick 1984). The California Fire Plan (California Department of Forestry and Fire Protection 1996) suggests increased use of prescribed fire in California's oak woodlands to reduce the severity of wildfires by limiting fuel accumulation and to manage livestock forage.

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In the central coast region of California (roughly the area between Santa Barbara and San Francisco extending to the coast mountain ranges approximately 80 km inland), the California Department of Forestry and Fire Protection (CDF) conducts prescribed burns on 1,000-4,000 ha annually (Parker, personal communication). The CDF presumes that prescribed fire benefits wildlife of oak woodland habitats, but no published research supports this assumption. Most research on effects of prescribed fire to wildlife and their habitats in California historically has been conducted in chaparral ecosystems (Lawrence 1966; Lillywhite North 1974; Longhurst 1978; Quinn 1979, 1983; Wirtz 1979, 1982). Except for a manuscript from this project (Vreeland and Tietje 1998), we are aware of no published research on effects of prescribed fire to California oak woodland habitats and associated wildlife species. Our objective was to quantify vegetation change and numerical response of small, non-game vertebrates to a prescribed fire conducted in mixed oak woodlands of the central coast region of California.

Materials and Methods

Study Area

We conducted this study at Camp Roberts (CR), California; a facility of the California Army National Guard located approximately 30 km from the Pacific Ocean in northern San Luis Obispo and southern Monterey counties. Topography at CR varies from flat to gently rolling hills and steep (>45° slope) hills. The climate of the study area is Mediterranean, characterized by cool, wet winters and hot, dry summers. Annual precipitation averages 38 cm (66-year range = 10.8-74.1 cm), falling almost exclusively as rain between November and March. Mean annual temperature averages 15.3°C. Summer high temperatures frequently approach 44°C; winter lows rarely fall below -6°C (U.S. Weather Bureau, Sacramento, California). Sheep grazing and military training occur in our study area, but are limited in extent, duration, and intensity. Fire has been excluded from the study area for >15 years (Brian Duke, CR Environmental Office, Camp Roberts, California). Our study sites were on slopes <20°, on north- to east-facing aspects, and 300-500 m elevation.

Camp Roberts comprises 17,000 ha, of which 41 percent is classified as oak woodland (Camp Roberts EMAP 1989). Three oak habitat types occur at CR: valley oak (*Quercus lobata*), coast live-oak (*Q. agrifolia*), and blue oak (*Q. douglasii*), with considerable overlap between coast live-oak and blue oak types. We used blue oak and mixed blue oak-coast live oak stands in the San Luis Obispo County portion of CR (Tietje and others 1997, Tietje and Vreeland 1997a). Blue oak sites were characterized by 40-60 percent canopy cover, <10 percent shrub cover, and >50 percent ground cover of exotic annual grasses. Blue oak was the dominant canopy species in the mixed blue oak-coast live-oak sites with a variable contribution (0-45 percent) of coast live oak. The mixed sites were characterized by 60-90 percent canopy cover, 10-30 percent shrub cover, and a well-developed, thick leaf litter layer with abundant herbs, forbs, and <30 percent grass cover.

Plants in the understory were primarily toyon (*Heteromeles arbutifolia*), redberry (*Rhamnus crocea*), poison oak (*Toxicodendron diversilobum*), and bigberry manzanita (*Arctoctsphylos glauca*). Small (0.25 ha) patches of chaparral (*Adenostoma fasciculatum*, *Baccharis pilularis, Ceanothus* spp., *Lotus scoparius* and *Salvia mellifera*) occurred on three study plots. Common forbs included hummingbird sage (*Salvia spathacea*), filaree (*Erodium* spp.), and fiddleneck

(*Amsinckia* spp.). Wild oats (*Avena* spp.), bromes (*Bromus* spp.), and fescues (*Festuca* spp.) dominated grassy openings of the woodland floor. Tietje and others (1997) and Tietje and Vreeland (1997a) give detailed descriptions of vegetative and habitat characteristics of our study sites.

Prescribed Fire

We selected two areas to receive a prescribed fire treatment. One area (hereafter "Burn 1") was 73 ha, the other area (hereafter "Burn 2") was 130 ha. The California Department of Forestry and Fire Protection and the Camp Roberts Fire Department burned these areas on consecutive days in October 1997. The perimeter was burned first, then the interiors were ignited using drip torches, and accelerants delivered from a helicopter. Surrounding unburned areas hereafter are referred to as "Ctrl" or "unburned areas."

Small Mammal Sampling

In winter 1996, we used a compass and meter tape to lay out an 8 by 8 grid with 15-m spacing (64 intersections) on each of 22 1.1-ha sampling plots. During May 1997-1999, we live-trapped small mammals on the plots by placing a single Sherman live trap at each of the 64 intersections. Plots were evenly divided between burned and unburned areas; six plots were in Burn 1 and five plots were in Burn 2. Four pairs of plots were approximately 40 m apart; the others were >100 m apart. Spatial separation between plots was adequate because <4 animals moved among plots during the study.[4] We trapped for five consecutive nights during 1997 and three consecutive nights during 1998 and 1999. We baited traps with horse feed ("COB": corn, oats, and barley laced with molasses), tagged animals with individually numbered ear tags, and released them at site of capture. We handled animals in accordance with University of California, Berkeley Animal Use Protocol No. R166-0199.

Breeding Bird Sampling

We conducted point-counts of breeding birds during March-April, 1997-1999. We used 86 50-m-radius point count stations located 150 m apart. Stations were evenly divided between burned (43 stations [13 stations were in Burn 1, 30 stations were in Burn 2]) and unburned areas (43 stations). We visited each station six times in each season. We rotated station visitations among start time, observer, and treatment. Two to four observers conducted counts in each year. We conducted counts for 10 minutes at each station between official sunrise and 1100 hours using standard breeding-bird survey protocols (Bibby and others 1992).

Amphibian and Reptile Sampling

We counted amphibians and reptiles under 136 61-cm by 61-cm by 1.27-cm plywood coverboards (DeGraaf and Yamasaki 1992, Grant and others 1992, Tietje and Vreeland 1997b) on each of nine 5.8-ha plots (8 by 17 grid, 30- by 15-m

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[4] Unpublished data supplied by W. D. Tietje.

spacing), established in 1993 for another study. Five plots were in the unburned area, two plots each were in Burn 1 and Burn 2. We checked each coverboard once every 7-10 days during late January-early May in 1995-1999. We used this size coverboard because we required thorough coverage throughout our plots and because larger coverboards warp and therefore may be less effective in the Mediterranean climate of our study area (Vreeland, personal observation). We first deployed coverboards in 1994 to allow them to weather for 6-9 months, dissipating chemicals used in their manufacture that might affect their use by amphibians and reptiles (Grant and others 1992). We had difficulty identifying slender salamanders (*Batrachoseps* spp.) (Scott, personal communication). California slender salamanders (*Batrachoseps attenuatus*) and black-bellied salamanders (*B. nigriventris*) potentially occur at CR, but cannot be distinguished in the field. Therefore we grouped them into one species category, hereafter "slender salamanders."

Vegetation Sampling

Within 2 months before and within 2-3 months after the prescribed fire, we sampled vegetation on the 11 1.1-ha small mammal sampling plots in the burned areas. We randomly located five 10-m-radius sampling stations on each plot. At 10 m in the cardinal directions from the central point of each station, we measured canopy cover with a concave spherical densiometer (Lemmon 1956), understory obstruction (an index to shrub cover) with a vegetation pole (Griffith and Youtie 1988) graduated in five 0.5-m sections, and ocularly estimated ground cover within 1 m^2 frames. Litter depth (an index to litter volume) was taken with a ruler (nearest 0.5 cm) at the center of the square frame. Within 10 m of the central point of each station, we counted the number of pieces of coarse woody debris (CWD, ≥1 m long and maximum diameter ≥10 cm), number of snags (≥1.37 m tall and ≥10 cm diameter at breast height), and number of dwellings (hereafter "houses") constructed by dusky-footed woodrats (*Neotoma fuscipes*).

Analyses

To assess fire intensity and coverage, we qualitatively described fire behavior according to CDF's fire intensity rating scale and we counted the number of grid intersections on small mammal trapping grids at which fire burned to within 1 m. In Vreeland and Tietje (1998), we conducted paired-sample *t*-tests to assess vegetation changes due to the fire. We considered differences significant at alpha=0.05. We repeat an abbreviated version of those vegetation results here, but direct the reader to Vreeland and Tietje (1998) for details on vegetation results.

Because we were unable to randomly select burned areas and because treatment replication was low (true replication was at the burn level, i.e., two burn replicates), our animal data cannot meet some assumptions of analyses of variance (ANOVA). Therefore, rather than conduct inappropriate, low-power statistical tests, we used means and 95 percent confidence intervals (CI) to assess numerical response of vertebrates to the prescribed fire. We selected one species to represent each of the four vertebrate taxa that we monitored (amphibians, reptiles, birds, mammals). We selected the representative species based on two characteristics: large relative abundance and potential for demonstrating change as a result of prescribed fire.

Relative species abundance was calculated for each experimental unit (plot or point count station), and then averaged for a treatment area (Burn 1, Burn 2, Ctrl). Because we have pre- and post-fire data on burned and unburned areas, pre-fire differences in relative abundance between burned and unburned areas are unimportant. The meaningful test of an effect of the fire is a comparison between relative abundance of a species on burned areas compared to unburned areas (Ctrl) before and after the fire. This is analogous to the interaction term in a 2-way ANOVA. Differences between treatment means were considered not statistically different if any portion of their 95 percent CI overlapped.

Results

Prescribed Fire

The California Department of Forestry and Fire Protection rated the prescribed fire as light to moderate in intensity (3-4 on a 10-point scale). Flame height generally was <1 m except in a few areas of decadent grasses, chaparral, or dense accumulations of CWD. Few mature trees died. The fire was patchily distributed and carried better through blue oak stands with abundant grass cover than through mixed oak stands with thick leaf litter and dense canopy cover. Mineral soil was mostly unexposed except in small areas with high fuel load (dense CWD, chaparral). Area burned on 1-ha plots averaged 46 percent (range 30 to 66 percent).

Vegetation

Understory obstruction (shrub cover) and grass cover were reduced by 7 percent and 70 percent, respectively ($P<0.05$). Much of the reduction in understory obstruction, however, resulted from our recording (as shrub cover) the obstruction by grass of the lower 0.5 m of the vegetation pole. Excluding this grass cover probably would result in no statistical reduction in understory (shrub) obstruction. Grass cover returned to pre-fire cover by one growing season after the fire. Canopy cover, number of snags, and litter depth did not change. Approximately 6 percent of the canopy was singed. Number of woodrat houses was reduced by 30 percent ($P<0.05$) and number of pieces of CWD was reduced by 35 percent ($P<0.05$). We recorded five new pieces of CWD in the 55 10-m vegetation plots. These pieces of CWD were created when roots of mature oaks were burned during the fire, causing the bole to fall to the ground. Vreeland and Tietje (1998) report detailed vegetation responses to the prescribed fire.

Small Mammals

We captured nine species of small mammals during 3 years of live trapping. Woodrats, piñon mice (*Peromyscus truei*), brush mice (*P. boylii*), and California mice (*P. californicus*) were the four most abundant species. Woodrats were the most frequently captured species (26.5 captures/100 trap-nights during 1997-1999). Relative abundance (captures/100 trap-nights) of woodrats on burned areas compared to the unburned areas did not change after the prescribed fire *(fig. 1)*. Relative abundance of woodrats was approximately 60 percent lower in 1998 and 1999 than in 1997, but this reduction was proportional among burned and unburned areas.

Confidence intervals consistently overlapped treatment means and other CI within and among years.

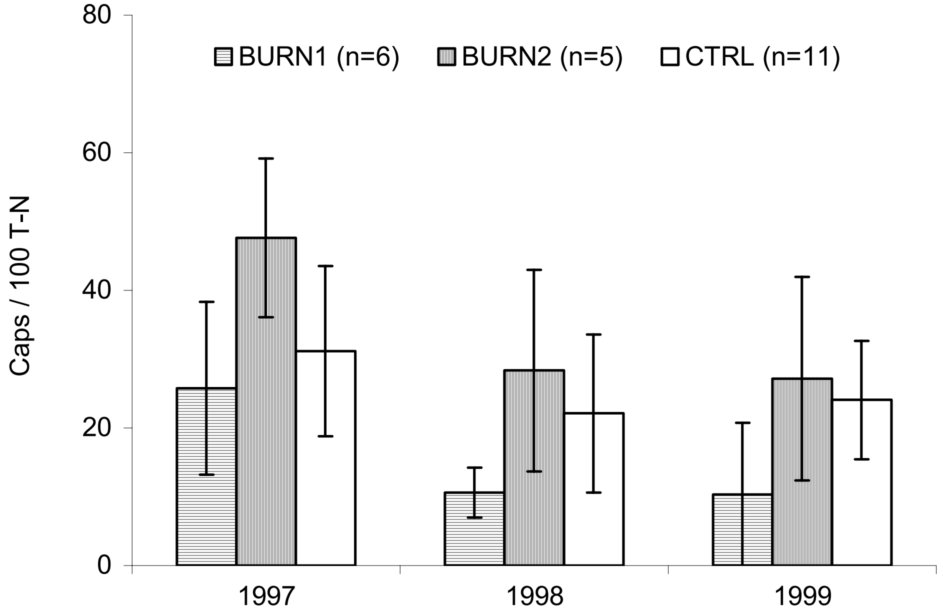

Figure 1—Dusky-footed woodrat abundance (captures per 100 trap-nights) in May 1997-1999 before and after an October 1997 prescribed fire in blue oak-coast live oak at Camp Roberts, California. Error bars are 95 percent confidence intervals.

Breeding Birds

We observed over 85 species of birds during the breeding season on the 86 point count stations. Dark-eyed juncos (*Junco hyemalis*) were one of the two most frequently observed species (1.7 observations/point/visit during 1997-1999, respectively). Relative abundance (mean number of observations/point) of juncos on burned areas compared to unburned areas did not change after the prescribed fire (*fig. 2*). We observed an approximately 80 percent increase in juncos 2 years post-fire, but this increase was proportional among burned and unburned areas. Juncos consistently were more abundant on Burn 1 than Ctrl, but the difference remained consistent before and after the fire. Other confidence intervals were narrow, but consistently overlapped treatment means and other CI within and among years.

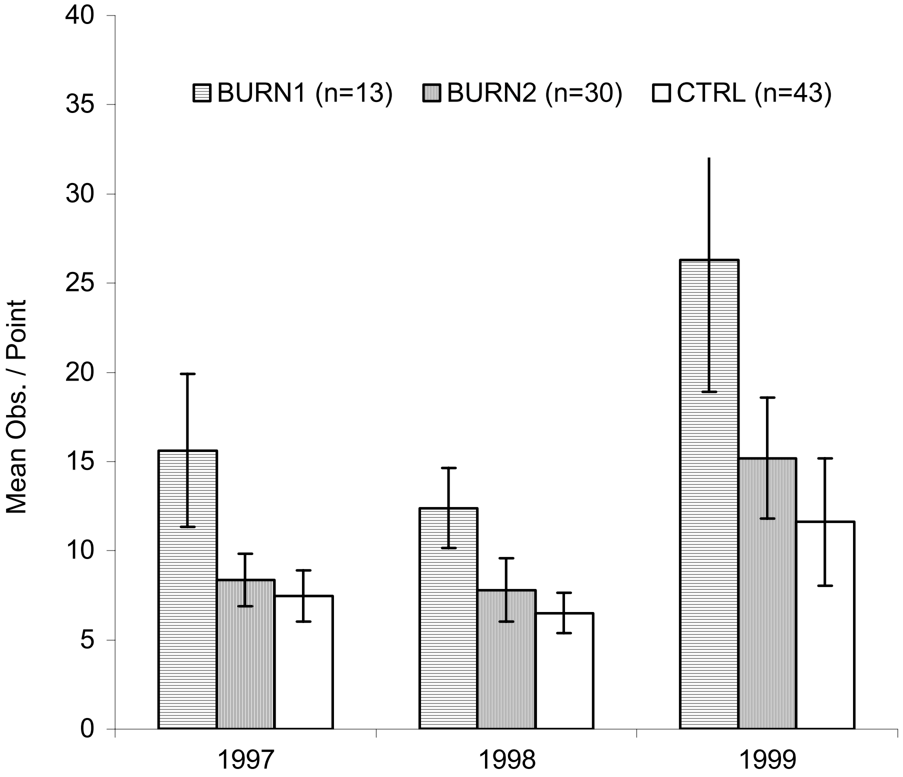

Figure 2—Dark-eyed junco abundance (mean number of observations per point) in March and April 1997-1999 before and after an October 1997 prescribed fire in blue oak-coast live oak woodlands at Camp Roberts, California. Error bars are 95 percent confidence intervals.

Amphibians and Reptiles

We observed four amphibian (two salamanders, one frog, one toad) and 11 reptile (five lizards, six snakes) species under plywood coverboards. Among amphibians, only slender salamanders were observed in appreciable numbers (1.74 observations/100 coverboard visits during 1995-1999). Relative abundance (number of observations/100 board-visits) of slender salamanders was similar on burned areas compared to unburned areas before and after the prescribed fire *(table 1)*. Except during 1999, slender salamanders were more abundant on Burn 1 than Burn 2 or Ctrl, but this pattern of relative abundance remained consistent among years before and after the prescribed fire. Confidence intervals were broad, frequently included zero and other treatment means, and overlapped other CI within and among years.

Western skinks (*Eumeces skiltonianus*) were the most frequently observed reptile species (3.96 observations/100 coverboard visits during 1995-1999). Relative abundance (number of observations/100 board-visits) of western skinks varied among years and among treatment areas within and among years, but was similar on burned areas compared to unburned areas before and after the prescribed fire *(table 1)*. Skink observation rate appeared to be increasing on Ctrl, decreasing on Burn 2, and irregular on Burn 1, but these trends began 2-3 years before the fire, and were not caused by nor interrupted by the fire. Confidence intervals were broad, frequently included zero and other treatment means, and overlapped other CI within and among years.

Table 1—*Relative abundance (mean, 95 percent CI) of slender salamanders and western skinks on burned and unburned areas before and after prescribed fire in blue oak–coast live oak woodlands at Camp Roberts, California, 1995–1999. The prescribed fire was conducted in October 1997. Pre-fire years are 1995–1997. See text for sample sizes.*

Year	Treatment	Slender salamander	Western skink
1995	Burn 1	8.6 (0–89.0)	2.6 (0–13.3)
	Burn 2	0.8 (0–7.7)	4.0 (0– 8.3)
	Ctrl	0.6 (0–1.4)	3.3 (0– 6.7)
1996	Burn 1	2.0 (0–15.1)	2.0 (0–12.3)
	Burn 2	1.0 (0–11.3)	3.4 (0–10.4)
	Ctrl	0.3 (0–0.6)	3.5 (0–7.0)
1997	Burn 1	2.9 (0–19.2)	1.7 (0–7.7)
	Burn 2	2.4 (0–21.6)	2.7 (0–9.7)
	Ctrl	1.0 (0–2.2)	4.8 (0.2–9.3)
1998	Burn 1	6.6 (0–52.4)	3.3 (0–26.1)
	Burn 2	3.2 (0–32.1)	2.4 (0–4.7)
	Ctrl	1.0 (0–2.2)	6.7 (0.3–13.0)
1999	Burn 1	1.8 (0–15.4)	2.8 (0–18.9)
	Burn 2	2.8 (0–33.1)	2.4 (0–15.6)
	Ctrl	0.4 (0–0.9)	6.7 (0–12.7)

Discussion

We detected no change in relative abundance of small mammals, breeding birds, amphibians, or reptiles after a light- to moderate-intensity prescribed fire in a California blue oak-coast live oak woodland. The low intensity fire resulted in generally marginal or short-term changes to the 13 vegetation characteristics that we measured. Only four habitat elements: grass, shrub cover, coarse woody debris, and woodrat houses were reduced significantly ($P<0.05$) by the fire, and these habitat alterations may not have been significant biologically. The significant removal of shrub cover was an artifact of our sampling method. Grass cover was 70 percent removed, but it grew back within a few months of the fire. Other habitat elements are also apparently more important than grass cover for habitat occupancy and the abundance of most of the small vertebrates that we monitored (Tietje and Vreeland 1997a). Although one of these habitat elements is coarse woody debris (Tietje and Vreeland 1997a), it is not surprising that the 35 percent reduction of coarse wood debris did not result in a detectable numeric change in relative abundance small vertebrates. Coarse woody debris was abundant throughout the study area and ample amounts likely remained to supply essential hiding, foraging, and breeding cover. Similarly, the availability of woodrat houses was likely not limiting after 30 percent were burned. Not all woodrat houses are occupied on the study area (Vreeland and

Tietje 1999) and the fire did not reach many of the houses in the densest habitats; therefore, few woodrats were forced to relocate to new areas or construct new houses after the fire. Responses to the fire were also minimal because small vertebrates have adapted to low intensity fire over the last millennia. Historically, fires were ignited by lightning or set intentionally by Early Americans to clear ground, aid in gathering acorns, and to drive game (as cited in Rossi 1980). They were frequent and rather low in intensity. Most small vertebrates have subterranean access or flee to avoid direct mortality.

The study has several shortcomings which compromise statistical inference. It was not practical or, in some cases possible, due to budget and feasibility constraints, to set up a true experiment. Fire control concerns rather than randomization dictated the location of our treatment areas (burn areas) and the treatment was not applied randomly to experimental units (small mammal and herpetofauna sampling plots or bird point count stations). The experimental units in our study, moreover, are pseudoreplicates within the burned (n=2) and unburned (n=1) areas), contributing to low statistical power (broad CI) for our data and rigorous statistical inference is compromised.

We believe our study, however, represents important, initial information on effects of prescribed fire to blue oak-coast live-oak woodland habitat and associated small, non-game vertebrates; and, our qualified conclusion of “no effect” is probably appropriate. We attempted to neutralize potential extraneous or nuisance variables not dealt with through proper control or randomization by adding time (before/after burning) as another control or reference. Therefore the natural changes in the abundance of the small vertebrates we monitored were less likely to be confused with a treatment effect. Annual fluctuations of monitored animals after the burn were within the range of abundances before the burn. “No effect” by species that we monitored was consistent within all four taxa (birds, small mammals, amphibians, reptiles) and across all pseudoreplicates of the treatment and control experimental units (22 small mammal plots, 86 bird point count stations, 9 herpetofaunal plots). Collectively, these support the supposition that, given similar blue-coast live oak woodland and fire intensity on the California central coast, one could expect little fire effect on the resident small vertebrates.

Management Implications

The CDF fire intensity scale (see table 1 in Tietje and others 2001) gives oak woodland managers and landowners an understanding of how to judge intensity based on the CDF criteria and where the intensity of our experimental fire at Camp Roberts lay. This fire was on the “light side” for prescribed burns conducted by CDF in oak woodland (Parker, personal communication). It provides strong subjective evidence that one could expect this result given this fire intensity in blue-coast live oak woodland similar in tree density and habitat structure to our study area at Camp Roberts. Prescribed fire that is light to moderate in intensity is also not detrimental to oak regeneration (Tietje and others 2001) but, overall, prescribed fire is probably beneficial by reducing resource competition from exotic annual grasses, stimulating shrub and tree health and vigor and, ultimately, mast production and overall habitat rejuvenation. Further study is needed to corroborate the results of this study and to evaluate the range of intensity of experimental burns and their effects on wildlife.

Acknowledgments

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Effects of Fire and Browsing on Regeneration of Blue Oak[1]

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Abstract

Blue oaks *(Quercus douglasii)* are not regenerating well over much of California. The roles of fire and browsing in regeneration are probably significant, but poorly understood. We burned two foothill blue oak woodland sites which contained significant numbers of small trees between 40 and 70 cm tall, then compared height growth over 14 years among 48 trees that were: a) unburned and unbrowsed, b) unburned but browsed, c) burned and browsed, and d) burned and unbrowsed. Fire completely killed and/or removed the tops, but all plants subsequently resprouted, creating an even-aged stem class. We found no evidence that fire stimulated regeneration. Protection from moderate browsing pressure by deer and cattle (approximately 75-80 percent of twigs to a height of 150 cm were browsed) favored regrowth and subsequent escape above the browse line, although some browsed plants also reached or exceeded browse height. Height growth differed significantly by site. On one site 11 of 12 unbrowsed plants had escaped to above the browse line, with several over 3 meters tall. On the other site growth was slower, but 9 of 11 surviving unbrowsed plants were above the browse line. Fourteen years after fire enough blue oaks were successfully recruited on both sites from the shrub into the sapling class to maintain or increase overall stand density.

Introduction

Blue oaks recruit successfully in some locations of the state but not others (Bartolome and others 1988). Several factors have been proposed to explain recruitment and regeneration patterns, including grazing or browsing pressure and fire. These two factors are linked. White (1966) suggested that reduced deer and livestock numbers about 1890 favored oak regeneration. Vankat and Major (1978)

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claimed that heavy livestock use in the late 1800s reduced herbaceous competition and fire frequency sufficiently to stimulate recruitment.

Although fire is generally considered a destructive disturbance in blue oak woodland (Griffin 1977) because it may kill mature trees, McClaran and Bartolome (1989) and Mensing (1992) found a strong positive association of the timing of apparent blue oak recruitment and fires. Because fire top-kills trees and concentrates stem ages from re-sprouts, a positive association of apparent recruitment and fire is not surprising but also does not eliminate the possibility of fire-induced stimulation of regeneration (McClaran and Bartolome 1989). Small blue oaks are rarely killed by fire and vigorously re-sprout (Tietje and others 2001). Once a small oak re-sprouts it is potentially subject to browsing pressure which can eventually kill the plant or retard escape as a recruit into the sapling or tree class (Muick and Bartolome 1988).

This study assessed the impact of browsing and burning on small blue oaks in moderately dense stands with more than 800 mm of annual precipitation. This type of site was selected because small plants with potential for recruitment are frequently present. Results are not applicable to drier and more open oak savannahs. Fire and browsing were chosen for treatment because management for regeneration must control those two factors. We hypothesized that the combination of protection from browsing and increased growth following fire would lead to recruitment of new trees into the overstory from the suppressed pool of small shrub-like oaks.

Study Areas

The Crowe Ranch (study area 1) is located in Lassen County east of Redding at an elevation of 800 meters. Precipitation averages 800 mm per year. Cattle normally graze lightly in the study area, which is primarily an upland included with irrigated pasture, but were excluded during the spring of the burn to allow fuel accumulation. Deer are locally common. The area is blue oak dominated at approximately 25 percent tree canopy cover. The study area had been burned under prescription in July 1981 to remove some oaks and brush for range improvement, therefore the site supports less tree cover than historically. Following the 1981 fire many blue oaks resprouted and were between 40 and 70 cm tall in 1986.

In July 1986 the Crowe Ranch study area was burned by the Lassen County Range Improvement Association as part of a 100 hectare prescribed burn. Conditions were good for a range improvement burn, with temperature at the start of the burn (1700 hrs) 33 degrees C and a relative humidity of 19 percent. Wind was less than 8 kph. The flame front at the study site measured 1.5 to 2 meters in dry grass fuel that weighed 2500 kg/ha. Conditions resulted in complete combustion of grass and tops of the small oaks. All small oaks were top killed. Post fire sampling was initiated in spring 1987.

The Ellis ranch (study area 2) is in Madera County near North Fork. The vegetation is similar to the Crowe ranch, with a blue oak canopy of about 25 percent. The study site had numerous small blue oaks between 50 and 70 cm tall which had regenerated following clearing of small trees in the mid-1970s and a range improvement burn in 1979. The site is at approximately 800 meters elevation and receives 800 mm of annual precipitation. The pasture is irregularly grazed moderately by cattle but was unused in the year preceding the fire. Deer are scarce in the area.

The Ellis ranch was burned in July 1987 as part of a 600-hectare range improvement burn conducted under the state Vegetation Management Program. Conditions for a range improvement burn were good, with the temperature at the start of the burn (1,000 hrs) 27 degrees C, at a relative humidity at 20 percent. Wind was less than 8 kph and grass fuels totaled 2,000 kg/ha. The flame front varied from 0.6 to 1.2 meters and most of the dry material was consumed, but some unburned grass and oak litter remained at the soil surface. All study plants were top killed. Postfire sampling began in spring 1988.

Methods

At each ranch 24 small blue oaks between 40 and 70 cm tall were selected for study. The 24 plants were divided into four groups of six plants each. Four treatments were: 1) unburned and unbrowsed, 2) unburned and browsed, 3) burned and unbrowsed, and 4) burned and browsed. The burn treatment was manipulated by construction of a fire-line which split the 24 plants into burned and unburned groups; the unbrowsed treatment by the random allocation of wire mesh cages to half of the plants in each burn treatment. Each plant was permanently marked with rebar and a metal tag. In midsummer prior to any treatment (July 1986 at the Crowe Ranch, July 1987 at the Ellis ranch), we measured each plant for height and maximum and minimum crown diameter.

Because we were interested in potential changes in growth form we also counted number of stem meristems on each plant by 10 cm height increments. Measurements were repeated for three years following the burns and again in 2000, 14 years after fire at the Crowe Ranch and 13 years after fire at the Ellis Ranch. Meristem counts were not repeated in 2000. Means were evaluated and compared for significant ($p<0.05$) differences with t-tests.

Results

The average height and meristem distribution pretreatment did not differ significantly for the two study areas. Burning removed the tops of small blue oaks, resulting in a decrease in average height *(figs. 1 and 2)*. Burned plants quickly resprouted and only one of the total of 48 plants died during the first 3 years. That was a burned and unbrowsed plant at the Crowe Ranch, which was likely killed by rodents in the second year of the study. By 2000 two more plants had died at the Crowe Ranch and two died at the Ellis Ranch in the intervening 13 years but no cause could be assigned. The total mortality during the study was 5/48 (10 percent) and not related to any particular treatment.

The resprouting pattern of burned plants, as reflected by meristem distribution, was one of rapid elevation of a few meristems in the first post burn year followed in the next 2 years by production of more lower meristems so that by the third post-burn year meristem distribution resembled that of unburned plants. At the Crowe Ranch, burned and grazed plants still showed significantly fewer meristems above 50 cm, while at Ellis the differences had disappeared by year three. Generally, however average plant height was the better response variable to evaluate treatment so we did not remeasure meristem distribution in 2000.

Height recovery from burning differed on the two sites. Changes in plant crown volume and diameter precisely followed the pattern of simple height measurements and will not be described separately. By the second year following burning at the Ellis Ranch, average heights of all treatments including burning significantly exceeded pretreatment *(fig. 1)*. Recovery took longer at the Crowe Ranch but was observed in all treatments to pretreatment heights by the third year *(fig. 2)*. Browsing protection significantly increased the rate of recovery for the first three years at the Ellis Ranch but not at the Crowe Ranch.

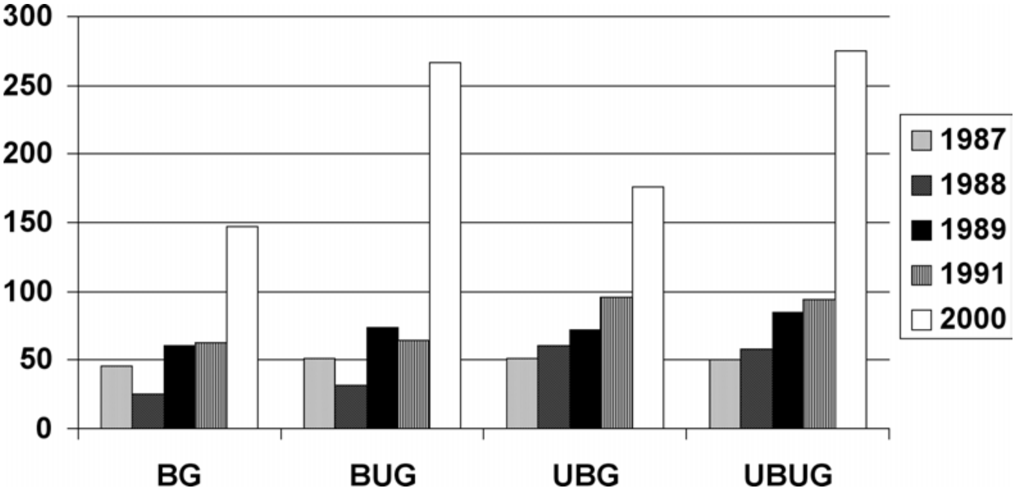

Figure 1—Average heights (cm) of small shrubby blue oaks at the Ellis Ranch measured prior to any treatment (1987), for three years after burning in summer of 1987 (1988-1991) and 13 years after fire (2000). Treatments are 1) Burned and browsed (BG), 2) Burned and unbrowsed (BUG), 3) Unburned and browsed (UBG), and 4) Unburned and unbrowsed (UBUG). Height differences between burned and unburned treatments were not significant ($p<0.05$, t-test) after 1988. Differences between browsed and unbrowsed treatments became significant in 1991 and were still significant in 2000.

After more than a decade, plants protected from browsing were significantly taller at both sites and early differences between burned and unburned plants had disappeared *(figs. 1* and *2)*. We saw no evidence that burning stimulated growth. Browsing at both sites extended to 150 cm and was estimated at 80 percent of the meristems below that level at the Ellis Ranch and 75 percent at the Crowe Ranch. In 2000 at Ellis, 11 of 12 unbrowsed plants had meristems above 150 cm and 4 of 10 browsed plants were above 150 cm. At the Crowe Ranch in 2000 only 1 of 12 grazed plants reached above 150 cm but 9 of 11 ungrazed had escaped to above the browse line.

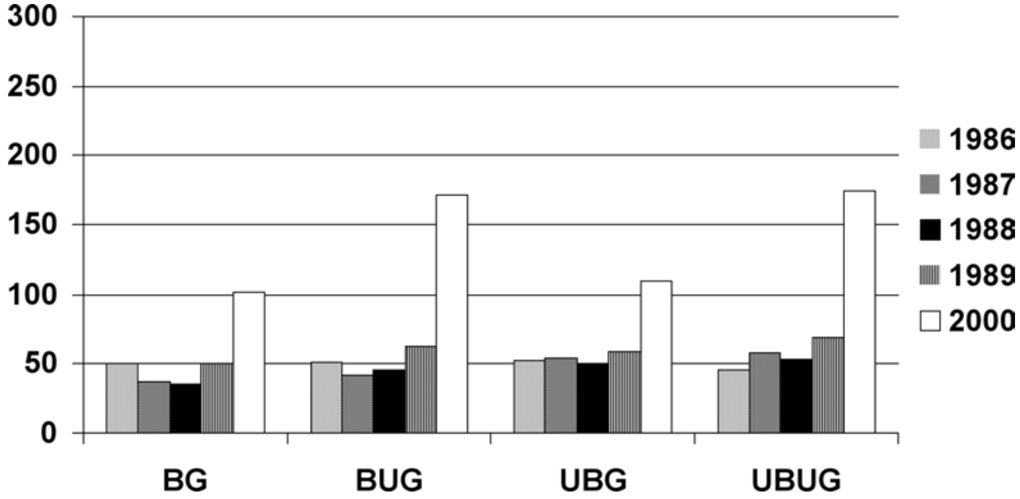

Figure 2—Average heights (cm) of small shrubby blue oaks at the Crowe Ranch measured prior to any treatment (1986), for three consecutive years after burning in summer of 1986 (1987-1989) and 14 years after fire (2000). Treatments are 1) Burned and browsed (BG), 2) Burned and unbrowsed (BUG), 3) Unburned and browsed (UBG), and 4) Unburned and unbrowsed (UBUG). Height differences between burned and unburned treatments were not significant ($P<0.05$, t-test) after 1988. Differences between browsed and unbrowsed treatments became significant in 1989 and were still significant in 2000.

Conclusions

The two sites differed considerably in plant response to treatment, with regrowth more rapid at the Ellis Ranch than at Crowe. The majority of plants at Ellis were above the browse line after 13 years, even unprotected plants. The cause of the differences between the sites is unknown, but shows that future research and recommendations for management need to account for probable considerable variability in response in different locations.

Fire appeared to lack any stimulatory effect on regrowth. We had hypothesized that burning combined with protection from browsing would speed elevation of meristems above the browse line. The results do not support this contention, plants grew best at both sites when protected from browsing and unburned.

Appropriate management for recruitment from sprouts will depend on growth rates for the specific site. At the Ellis ranch, under existing browsing pressure and projected early growth rates, even some unprotected sprouts would have exceeded the browse line after six or seven years. The major concern for enhancement of tree recruitment should be keeping the area free of a fire during that period to ensure successful regeneration into the sapling stage. At the Crowe ranch, for successful regeneration into the sapling stage, small plants must be protected from burning and browsing for ten or more years.

Fires, whether natural or prescribed, set back the growth of small shrubby blue oaks and do not result in a stimulation of regrowth and are not a stimulant to regeneration. Fires are also not necessarily incompatible with regeneration if the fire frequency is low and/or regrowth rates are high enough. The association of fires with episodes of regeneration in blue oaks as observed by McClaran and Bartolome (1989) is more a result of the effect of fire on apparent age class of the stems of resprouting plants than a stimulatory effect. Browsing pressure probably plays an important role in the sites studied by suppressing height growth whether or not the plants are burned. Suppression by browsing appeared sufficient to prevent regeneration of unprotected plants at Crowe but not at Ellis. Because no mature trees died during the study on either site, recruitment from small shrubby blue oaks increased overall density of sapling and larger trees on the sites.

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Development and Fire Trends in Oak Woodlands of the Northwestern Sierra Nevada Foothills[1]

James G. Spero[2]

Abstract

Human development appears to present a larger threat to the long-term persistence of California's hardwood rangelands than fire in terms of likely ecological significance. This paper describes of the California Department of Forestry and Fire Protection's Fire and Resource Assessment Program (FRAP) projections of human development and fire occurrence and explores trends in the incidence of fire and development on woodland areas historically dominated by oak species. Previous FRAP work on fire probability on about 3 million acres of private lands in the northwestern Sierra Nevada foothills provides a small-scale model of comparison for these forecasts. FRAP's methods combine historical (1950-1990) block group housing density estimates based on the 1990 Census with decadal housing projections (2000-2040) derived from Department of Finance county population projections. County housing projections are allocated to 9.6 square mile grid cells based on their share of county housing growth between 1980 and 1990. The primary purpose is to produce estimates with a low level of error in the acreage that is projected to attain at least a dispersed level of residential land use. Overlaying development projections on a 1945-vintage vegetation map yields tables of vegetated acres developed from 1950 to 2040. In this analysis, developed areas are defined as having reached a housing density of at least one house per 20 acres and presumed to present a potential for ecological impact. Current and future "footprints" of development within the study area are compared to the expected amount of fire over time to provide a context for evaluating the ecological significance of development and fire in hardwood ecosystems. By 2040, an estimated 507,000 acres (22 percent of the ~2.3 million acres of 1945-era oak woodland in the study area) will be developed. This regional rate of development is higher than for all oak woodlands statewide, which show 16 percent development by 2040. In the study area, hardwoods burned on the average ~0.5 percent per year where development density was less than one house per 20 acres. In areas of higher development density, the rate of burning was about 0.2 percent. An estimated 411,812 acres will burn in the 2000-2040 period. Driving this estimate are area characteristics, such as predominating vegetation life form and developed/undeveloped status. Plausible reasons for reduced fire occurrence in developed areas include quicker detection, more fire suppression resources, improved access and fire safe development, and modified vegetation composition and structure that lessens fire hazard. Assuming 30 percent and 5 percent net mortality from development and fire, respectively, FRAP researchers estimate that by 2040, about 80,000 acres (about 4 percent of the vegetation extant in 2000) might be lost due to development (about 60,000 acres from development, about 20,000 acres from fire). Long-term ecological impacts are perhaps more permanent with development than with fire, however, both fire suppression and land development policies will help shape the future of quickly developing

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foothill ecosystems. This analysis is a work in progress by the author and FRAP. Conclusions, data, and discussion are those of the author and FRAP.

Introduction

The land use impacts of population growth affect a number of responsibilities of the California Department of Forestry and Fire Protection (CDF). Expanded residential use of wildland changes the fire protection needs in terms of public safety, assets at risk, patterns of fire ignitions, and the deployment of new state and local fire service resources. Expanded residential use within forest and woodland areas also affects a variety of resource management activities, such as forest management, prescribed burning, and other forms of vegetation management and watershed protection activities. Changing residential use patterns also change the overall stresses on many wildlife species that depend on a matrix of reserved, managed, and developed land and water areas; local definitions of important open space; local and regional tax bases, and other factors.

To effectively assess trends and potential responses, it is useful to have a systematic approach towards projecting land use impacts of population growth. To help envision these resource management challenges, FRAP applies methods pioneered by Tim Duane for the Sierra Nevada Ecosystem Project (Duane 1996) to map the progression of development (housing density) from 1940 to 1990 across the entire State of California. Overlaying FRAP's map on a circa-1945 vegetation map allows FRAP researchers to map and plot trends in 20th Century development within grassland, shrub land, woodland, and conifer ecosystems. To generate a future scenario FRAP researchers generalize the progression of development map to 5,000-meter square grid cells. This second map contains allocations of Department of Finance (DOF) projections that are based on within-county housing count changes over the 1980-1990 period.

Tables of vegetated area developed by decade from 1950 to 2040 are created by combining vegetation overlay results from both progression of development maps (after adjustments to remove bias introduced by the change in scale).

For this paper, FRAP staff extract data pertaining to hardwood woodland types and report historical and projected development trends (1950-2040) both statewide and on the private ownership lands in a northwestern portion of the Sierra Nevada foothills. In the Sierra Nevada microcosm, estimates of fire occurrence in developed and undeveloped areas have already been produced.

Wildfire's role in hardwood ecology is unclear. Blue oak (*Quercus douglasii*), the most abundant hardwood forest type in California, has sapling populations that may be insufficient to maintain current stand densities (Bolsinger 1988, Muick and Bartolome 1987, Swiecki 1999). Although many species of native California oaks are relatively fire resistant, either due to innate low fuel conditions or to vegetative adaptation, fire may not play as much of a role in regeneration as once thought, neither enabling nor preventing regeneration (Bartolome and others 2002, Lang 1988). However, frequent fires can compromise re-sprouting from saplings and seedling advance regeneration. According to Swiecki: "A combination of frequent fires and annual livestock grazing would…be a prescription for eliminating blue oak regeneration." Even though in the past 50 years the amount of wildfire in this study area has been moderated by fire suppression and other factors resulting from rural development, prudence dictates continued awareness and concern about wildfire as a potential threat to hardwood resources.

The relationship between human development and fire is also complex. More people can logically mean an increase in the potential for ignitions, but FRAP's fire analysis shows that fire frequency based on area burned is lower in developed areas surrounding undeveloped wildland areas. FRAP researchers believe this is due to fire suppression and other factors such as roads, irrigation, and vegetation modification, that are a result of human development.

For the Sierra-specific analysis FRAP researchers apply estimates of mean annual wildfire occurrence to both developed and non-developed hardwood lands to 2040. Calculated fire rotation periods (expressed as percent area burned per year) for landscapes stratified to reflect different combinations of vegetation types and developed/undeveloped status evolved from a 48-year history of wildfires (coupled with vegetation and housing density information). Potential changes to oak woodlands arising from development are then inferred.

Methods

The statewide historical "Progression of Development" map (*fig.1*) is a consistent picture of development trends across all of California, depicting the location of developed and mixed urban/wildland interface within U.S. Census (1990) "split" census Block Groups by decade over the period 1940-1990. A block group is a cluster of census blocks within a census tract and contain between 600 and 3,000 people, with an optimum size of 1,500 people. Block Groups may be split along city and other administrative boundaries. The source of the historical housing counts is data from the 1990 Census "long form" survey question "Year Structure Built" for which respondents indicated the decade in which their home was built. Homes demolished and not rebuilt prior to the Census are not reflected in these data; therefore, there is some underestimation of housing density in earlier decades. Because impacts on wildlife habitat due to fragmentation by roads and other artifacts of rural development can occur even if very little acreage is directly converted to urban land uses (McBride and others 1996, Saving and Greenwood 2002, Scott 2000), this study uses a housing density threshold of one house per 20 acres to encompass potentially impacted rural residential lands as well as more densely settled areas. Beyond this threshold are constraints on ecosystem management, increased chances for habitat degradation, and increases in the potential for housing and other asset losses due to wildfire.

To create a map of future housing density this study uses the Share method (Smith and others 2001), also called the apportionment method (Pittenger 1976, White 1954). First, census block group housing counts are averaged to a uniform 9.65 square mile (5,000 m by 5,000 m) grid and then countywide DOF growth projections are allocated in the same proportions as observed in existing data for the period 1980-1990. At the block group scale, this simple model does not work well in highly urbanized areas because it does not explain a variety of site-specific factors, such as constraints on land availability, changing conditions in the building market, and urban growth policies. The spatial re-sampling tends to average housing counts in very small (i.e., highly urbanized) block groups, reducing the decade-to-decade variability in the data, and prediction errors fall to acceptable levels. Moreover, the resulting map (8,405 cells) still has enough spatial resolution for analysis at bioregional scales.

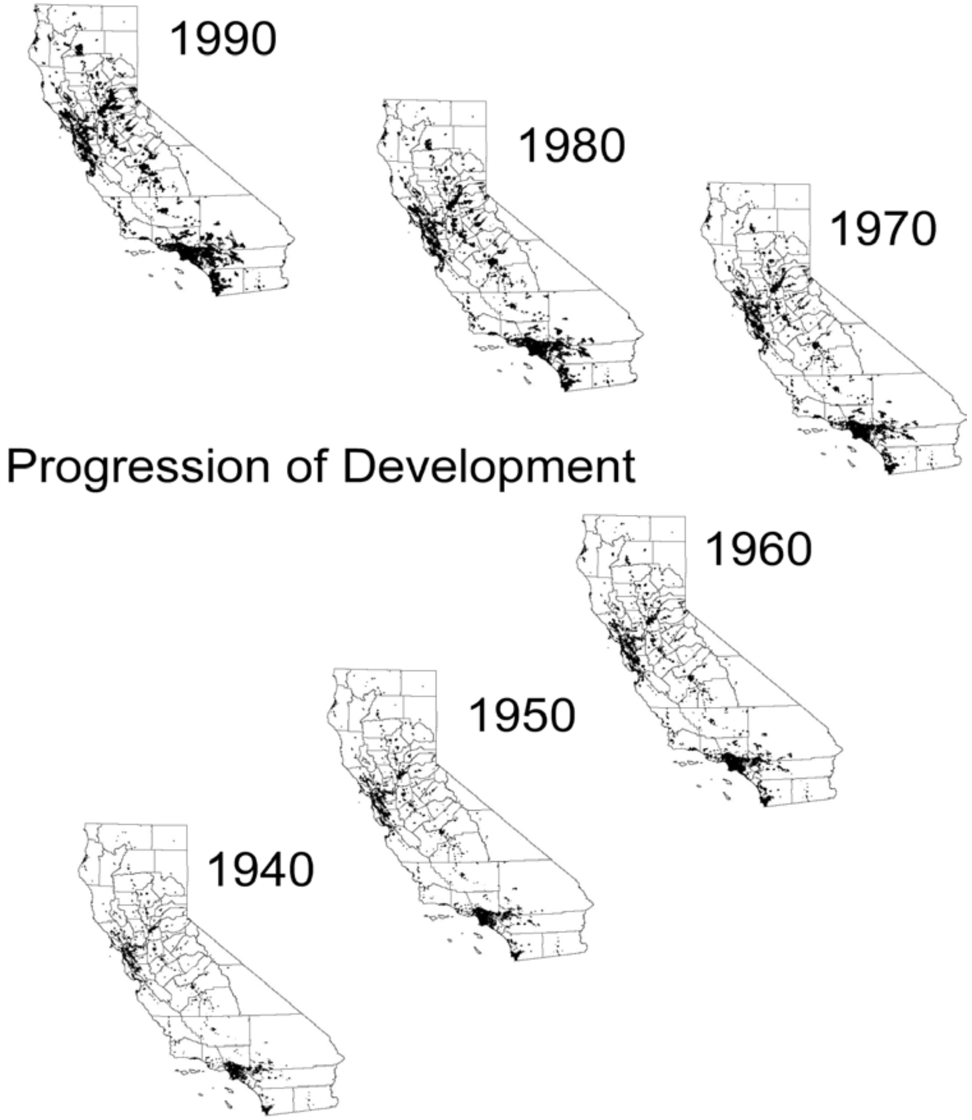

Figure 1—Maps of progression of development 1940-1990.

For the decades 2000, 2010, 2020, 2030, and 2040, this study converts DOF county population estimates to housing estimates using the 1990 countywide ratio of houses to people and apportions the new housing increments to each county's grid cells in the same proportions as in the 1980-1990 period. For example, to allocate projected county growth from 1990 to 2000 to a grid cell, this study multiplies that growth increment by the proportion of 1980-1990 growth captured by that grid cell (the growth factor), as in equation (1):

$$2000-1990i \approx \sum 2000-1990i \times \frac{1990-1980i}{\sum 1990-1980} \tag{1}$$

The increment of growth in cell *i* during the decade 1990 to 2000 equals its historical expected share of county growth, i.e., the total county growth from 1990 to 2000 times the proportion of the 1980 to 1990 growth captured by cell *i*.

For example, if a grid cell that had 1,000 houses in 1990 had captured 0.25 percent of the 1980-1990 county growth, and the DOF-based projection for that county for 1990-2000 was 100,000 houses, then the year 2000 estimate for that grid cell would be 1,000+(0.0025*100,000)=1,250 houses.

To create the future housing density map (*fig. 2*) we apply 1980-1990 growth factors to DOF county growth expectations for between 2000 and 2010 and add the results to the cell's expected housing count for 2000. We repeat these steps iteratively for calculations of 2020, 2030, and 2040 housing counts always using the 1980-1990 growth factor.

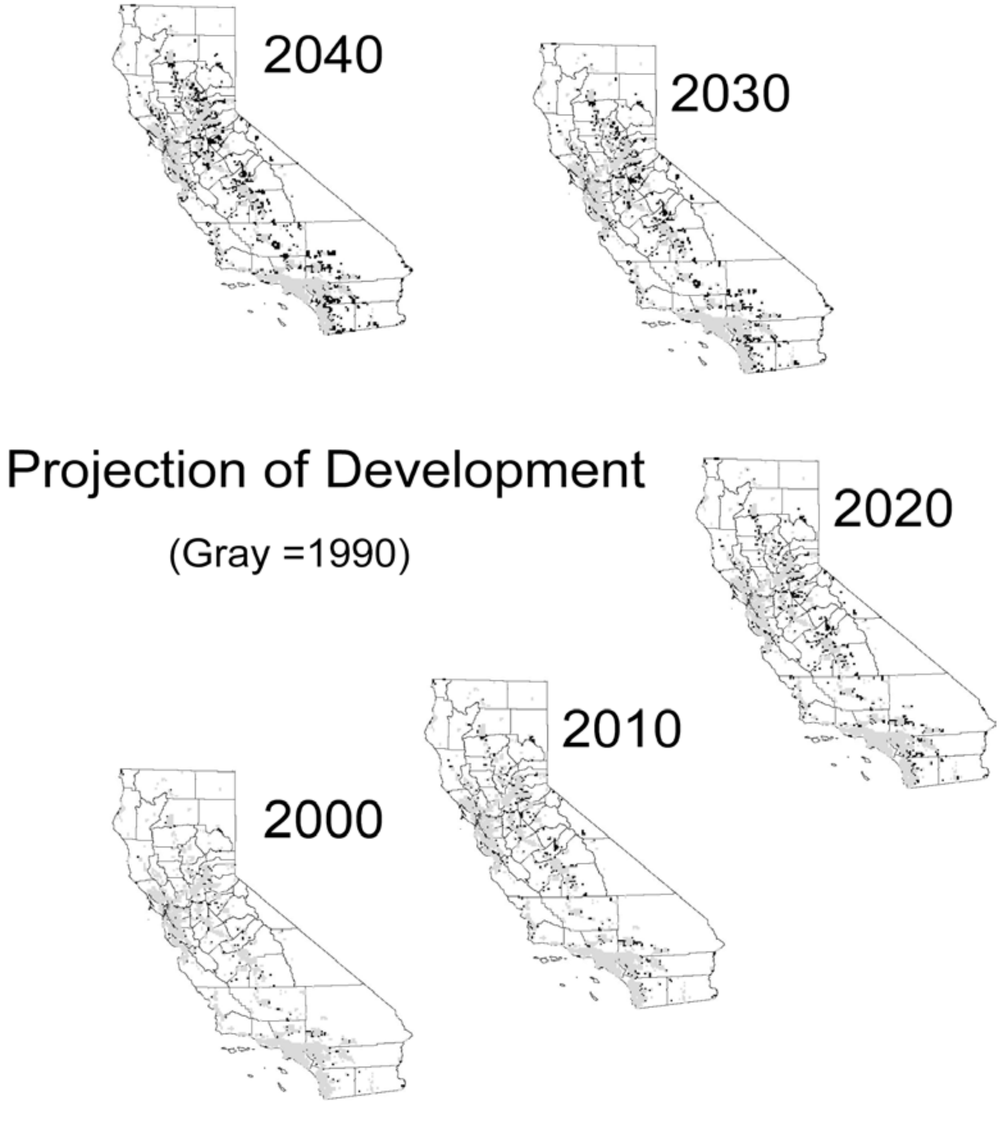

Figure 2—Maps of projection of development to 2040.

To test the accuracy of the growth factor variable, we implement the Share Model to split Block Group, Census Tract, and grid cell data using ordinary least squares regression techniques (*table 1*). The form of the model for creating a growth scenario for 1980 to 1990 (which is the most recent period that can be verified from the map data) is shown by equation (2):

$$1990-1980i \approx \sum 1990-1980i \times \frac{1980-1970i}{\sum 1980-1970} \qquad (2)$$

Table 1—*Regression analysis results on fit of share model for predicting 1990 housing count.*

Map	R^2	P	N
Census Block Groups			
Original	0.17	<0.0001	27,146
Log Transform	0.44	<0.0001	
Census Tracts			
Original	0.32	<0.0001	9,218
Log Transform	0.71	<0.0001	
5000-meter Grid Cells			
Original	0.7	<0.0001	8,780
Log Transform	0.88	<0.0001	

Regressions compare the actual growth of housing from 1980 to 1990 in a map polygon or grid cell (the dependant variable) with housing counts calculated using the expected share as the independent variable. Because both dependant and independent variables are highly and positively skewed, FRAP researchers also examined logarithmic transformations.

Model fit (R^2) improves for tracts and 5,000-meter grid cells (*table 1*). In the non-log transformed grid cell model the expected share for 1990 explains 70 percent of the variation in actual housing increase in 1990. This result is quite adequate for the scale of analyses envisioned. The significant P values are not surprising because the coefficients measure the entire population (Studenmund and Cassidy 1987). These statistics indicate that areas with higher proportions of growth in the 1970-1980 period show greater absolute growth in the period 1980-1990. We could have also shown that the process is consistent when using different sets of decadal data. For example, 1970s growth is predicted by 1960s share; 1960s growth by 1950s share, and so on. Thus, the 1990 results are consistent with a general pattern in the data over time.

A histogram comparing actual and modeled data by housing density class shows a close correspondence (*fig. 3*). The classes, numbered 1-8 correspond to housing density ranges as follows: (1) Less than 1 housing unit per 160 acres, (2) 1/160 to

1/40 acres, (3) >1/40 to 1/20 acres, (4) >1/20 to 1/10 acres, (5) >1/10 to 1/5 acres, (6) >1/5 to 1 per acre, (7) >1 per acre to 5 per acre, (8) Greater than 5 per acre.

Figure 3—Frequency of grid cell counts (actual, predicted housing density class).

The Share Model is limited to areas with at least some history of growth; hence it does not predict the emergence of new growth centers. That is, grid cells with no growth from 1980-1990 will continue to remain static through time. FRAP researchers are considering how this model might be used in combination with a more detailed urban growth models such as CUF-II (Landis 1995), which reflect underlying development probability but are difficult to calibrate for rural areas.

By overlaying a vegetation map (Pacific Forest Trust 1997) that shows the location of forests, rangelands, and agricultural areas shortly after World War II on the progression of development maps, the area of each vegetation type falling under the footprint of development over time is estimated. The vegetation base map is from the Vegetation Type Map (VTM) Survey, conducted between 1929 and 1934 by the U.S. Forest and Range Experiment Station, Berkeley and updated in 1945. We call this map "Weislander" after A. E. Weislander, the Survey's director. The original Weislander maps were at a scale of approximately 1:64000. The four broad vegetation classifications—forest, range, agriculture, and barren—reflect the historical perspective towards potential land uses. *Figure 4* shows the Weislander vegetation classification Woodland-grass with the Sierra Bioregion and northwestern Sierra Nevada fire study area boundaries.

Because the Weislander vegetation map did not exclude urban areas (for example, the Weislander "Agriculture" label includes Urban and Industrial land uses) FRAP researchers subtract acres under the 1940-development footprint (at 1 house per 20 acres for consistency) to leave a base map of circa-1940 vegetation. Two Weislander overlays are needed to produce tables of 1945-era vegetation developed by decade: one using census block groups and the other using the 5,000-meter grid.

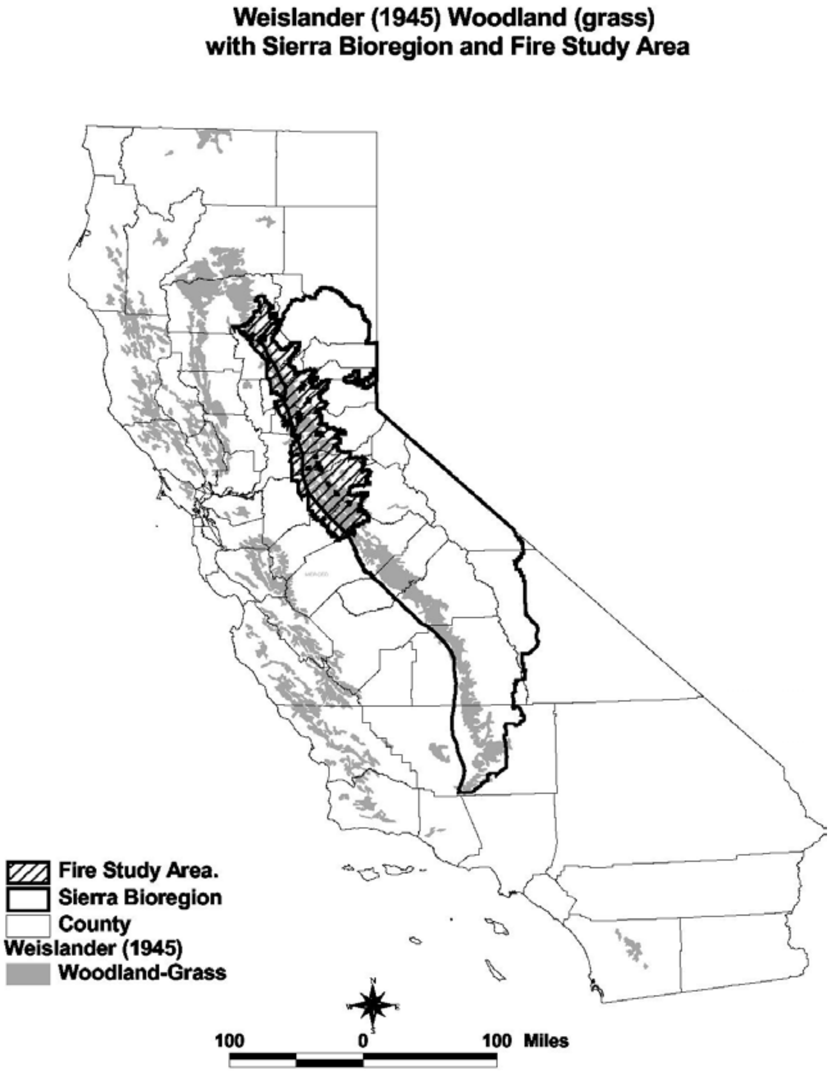

Figure 4—Map of Weislander Woodland-Grass vegetation, Sierra Bioregion, fire study area.

In constructing tables of development over time, the census block group/vegetation overlay provides the data for 1950 through 1990 while decades 2000 through 2040 are based on the 5,000-meter grid/vegetation overlay, with a calibration adjustment to correct for bias due to the change in scale. As mentioned earlier, the need for two different overlays arises because the two maps yield different results due to the effects of averaging. For example, the number of developed acres in 1990 (and earlier decades) differs between the two maps because small areas of high housing density measured at the block group level result in a developed label being placed on a grid cell of greater size. To deflate the grid-based results, we use a multiplier based on the ratio between the developed acres totals from the two maps for 1990. This multiplier adjusts developed acres for 2000, 2010, 2020, 2030, and 2040 and makes the grid-based results consistent with the 1990 and earlier data.

Intuitively, population gains mean that the agents of human-caused fires are more numerous, and it is logical to consider the possibility of an increase in the potential for more wildfire ignitions. The actual amount of fire depends on many factors such as weather, vegetation characteristics and conditions, topography, criminal activity (arson), and fire suppression. While infrequent "large" fires account for most of the area burned by wildfire (Strauss and others 1989, California Department of Forestry and Fire Protection 2000) most fires are stopped before they can become large and damaging. According to the CDF's Wildfire Activity Statistics for 2000, 26 fires listed as "large and damaging" burned 216,157 acres, or 73 percent of the total of 295,026 acres burned by 9,685 wildfires in all California wildland fire jurisdictions. The 26 fires represent a mere 0.3 percent of the total number of fires.

Our analysis of wildfire perimeter data on private ownership lands in the foothill areas of the Northwestern Sierra Nevada was needed to provide fire occurrence inputs for a model of fire effects on houses in El Dorado County (Greenwood 1999). In that model, the annual probability of burning an acre in a large fire is multiplied by the conditional probability of house loss and by the number of houses to produce estimates of expected house loss.

Available fire risk probability models produced for the Sierra Nevada Ecosystem (McKelvey and Busse 1996) were not designed for analysis of the predominantly lower elevations more characteristic of private lands. Therefore, FRAP researchers calculated mean annual fire rotation for various combinations of vegetation type (measured at the life-form level—conifer, mixed hardwood/conifer, hardwood, shrub, grass) and development status (developed – at least one house per 20 acres, undeveloped – less than one house per 20 acres). Results suggest that that wildfire protection and other factors have made a difference in fire occurrence rates in developed areas as compared to non-developed areas.

Computation of fire probability involves querying landscape attributes, linking burned areas to both a vegetation type and historical (decadal) housing density class consistent with the date of the fire (*table 2*). Earlier, FRAP used a related approach to map large fire probability in the Sierra Nevada bioregion (Sapsis and others 1996). For this analysis, however, FRAP researchers created landscape "strata" using FRAP's Arc/Info Geographic Information System (GIS)—polygons produced from the intersected boundaries of Widllife Habitat Relationships (WHR) vegetation data, census split Block Groups labeled with housing density for each decade from 1940 to 1990, and historical fire perimeters for the period 1950-1997. Most of the woodland vegetation data used in this analysis comes from 1997 imagery mapped by Pacific Meridian Resources (PMR) under contract with CDF and the USDA Forest Service. The fire perimeter data are for fires that burned at least 300 acres. Only areas that actually burned within the study area are calculated.

Table 2—*Housing density year to fire start year crosswalk.*

Fire year	Housing density year
1950-54	1950
1955-64	1960
1965-74	1970
1975-84	1980
1985-97	1990

Average fire probability for each stratum was calculated by computing the fire rotation period (FR). FR is the number of years required to burn an area equivalent to the size of that stratum. To calculate the FR, divide the average annual acres burned in stratum i into the total number of acres in the stratum, as shown in equation (3).

FR (years)= Total Area of Stratum/Average Annual Acres Burned (3)

The reciprocal of FR (1/FR) is the average probability of an acre burning in any year, referred to henceforth as p(burn). Multiplying an area's size in acres by its p(burn) gives the average annual number of acres burned.

Results—Statewide, Northwestern Sierran Foothills

Development Trends

Since the 1940s, statewide development trends have shifted from a concentration on agricultural lands to rangelands and forests. Of the approximately 7.5 million acres of statewide private range classified as Woodland-Grass by Weislander (1945), 7 percent was developed at a density of one house per 20 acres or greater by 1990. By 2040, 16 percent of the 1945-era hardwood vegetation could experience this level of development (*fig. 5*). This net increase of 9 percent reflects acres newly developed.

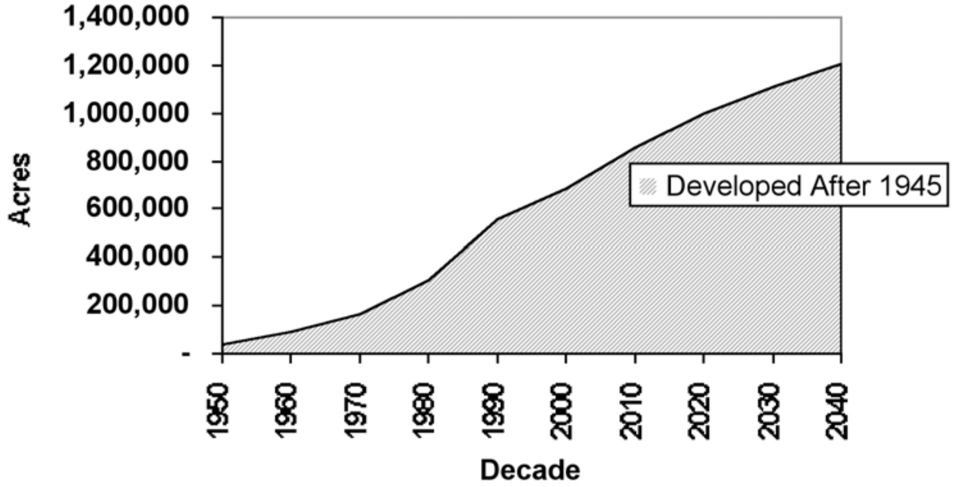

Figure 5—Development of private hardwood lands in California 1950-2040. In California, development will have occurred on 16 percent of the habitable 1945 Woodland-Grass land base by 2040. Undeveloped acres in 1945: 7,472,979.

These trends are more pronounced in the Northwestern Sierra foothills. The approximately 2.3 million acres of private land classified as Woodland-Grass by Weislander (1945), about 507,000 acres (22 percent) is expected to become developed by 2040 (*fig. 6*). Knowing that development is moving at a faster pace in the Sierra study area as compared to California hardwoods as a whole (a marginal increase of 6 percent) emphasizes heightened concern about impacts on important hardwood species.

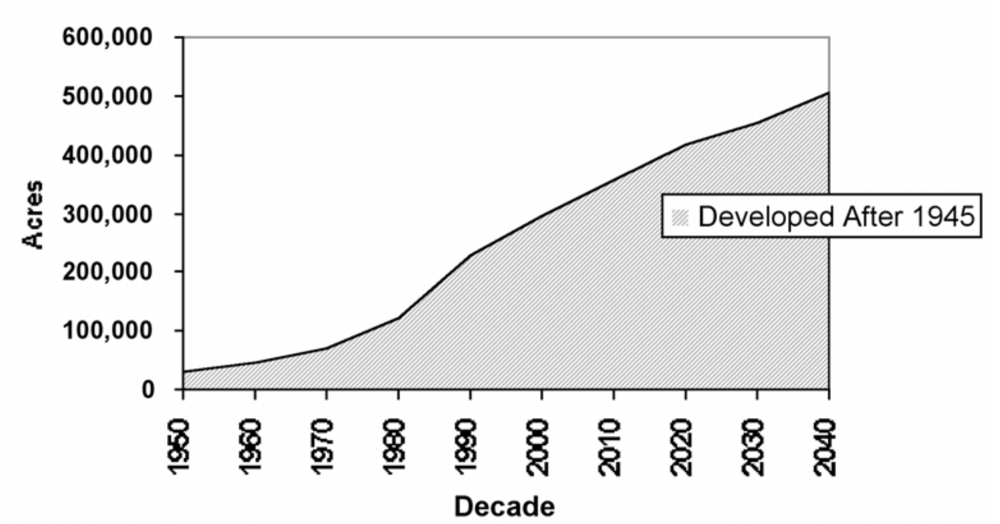

Figure 6—Development of private hardwood lands in the northwestern Sierra foothills fire study area 1950-2040. In the Sierra fire study area, development will have occurred on 22 percent of the habitable 1945 Woodland-Grass land base by 2040. Undeveloped acres in 1945: 2,287,753.

Fire Trends

Over the 48-year period from 1950 to 1997 a total of 529,824 acres burned in the roughly three million acre northwestern Sierra Nevada study area in all vegetation types (11,038 acres per year on the average or about 0.4 percent per year overall). Calculation from the Vegetation-only strata showed highest fire frequencies in the Shrub type (0.8 percent/year), followed by Hardwood and Grass (0.4 percent), Mixed Hardwood/Conifer (0.3 percent) and Conifer (0.1 percent). For Housing density-only strata, developed areas burned at 0.2 percent per year—half the 0.4 percent/year rate of burning in undeveloped areas. Combined, vegetation/housing density strata had substantially lower rates of burning in developed areas (with the exception of Conifer) than in undeveloped areas (*table 3*).

Table 3—*Fire rotation period (years) and annual wildfire probability [p(burn)] for vegetation strata by development status and overall.*

	Developed		Undeveloped		Any	
Vegetation type	**FR (yrs)**	**p(burn)**	**FR (yrs)**	**p(burn)**	**FR (yrs)**	**p(burn)**
Shrub	258	0.004	120	0.008	126	0.008
Hardwood	658	0.002	218	0.005	233	0.004
Grass	712	0.001	254	0.004	262	0.004
Mixed hardwood/conifer	802	0.001	312	0.003	333	0.003
Conifer	868	0.001	821	0.001	825	0.001

In the combined Hardwood/Developed stratum, annual wildfire probability was measured at 0.002 (0.2 percent per year) while for Hardwood/Undeveloped stratum it was 0.005 (0.5 percent). A one-tailed t-test on annual acres burned per 1,000 acres in both strata was significant (T=–2.14, P=0.0174). Overall, 172,080 acres burned in the 1950-1997 period.

Calculation of Weislander Woodland-grass acres burned in the 2000 to 2040 period (411,812) shows a decline over time. The number of acres in each land class (developed, undeveloped) is multiplied by its respective annual probability of burning and the products are summed (*table 4*).

Table 4—*Calculated burned area 2000-2040 for Sierra study area*

	Acres of woodland (grass)		x	p (burn)	=	Burned area
Year	**Developed**	**Undeveloped**	**Dev (0.002)**	**Undev (0.005)**	**Per year**	**Decade**
2000-10	294,591	1,993,163	589	9,966	10,555	105,550
2010-20	356,610	1,931,143	713	9,656	10,369	103,689
2020-30	418,629	1,869,124	837	9,346	10,183	101,829
2030-40	454,807	1,832,947	910	9,165	10,074	100,743
					Total area burned 2000-2040:	411,812
					40-year average:	10,295

Discussion

Future cumulative effects on habitat quality due to fire and development are difficult to predict. Because the predominant woodland species in this region (blue oak, interior live oak, canyon live oak) are all highly adapted to fire, development is much more likely to lead to persistent and cumulative impacts on oak woodlands. Urban development affects habitat adversely. Once you have smaller than 40-acre parcels with houses, driveways, fences, pets, etc., the chance of it functioning as habitat for a wide range of species diminishes rapidly (Shilling 2001).

Nevertheless, even low intensity fires can result in substantial oak woodland mortality. Swiecki and Bernhardt found that a relatively light grassfire that burned an oak stand in 1996 killed 6 percent of saplings and almost all saplings “less than 150 cm tall and/or with basal diameters of less than 5 cm were completely topkilled.” They found that nearly a year after the fire, “post-fire shoot biomass was clearly much lower than prefire biomass for all but the smallest topkilled saplings” and also that “saplings were least likely to occur in plots that had experienced multiple fires over a five year period” (Swiecki and Bernhardt 1999). Long-term effects of fire on oak woodland persistence are still unknown, however.

The amount of fire is predicted to decline over time (*table 4*) due to increasing portions of land area reaching developed status and the associated lower fire occurrence rates for these areas. It is assumed that the relationship of ignitions, detection, and fire service response in the future will be similar to the historical period on which the fire occurrence study is based.

Only a fraction of all fires burn with enough intensity to kill trees, or to prevent regeneration (either alone or through interactions with post fire herbivory/grazing).

Nevertheless, hardwood mortality presumably negatively affects habitat quality for a variety of species. Assuming 5 percent net mortality from fire and 30 percent net mortality from development, losses from development (63,569 acres) would be more than three times the losses due to wildfire (20,590 acres) *(figs. 7 and 8)*. Is a total net loss of 84,160 acres of Sierran hardwoods ecologically important? After all, this is a mere 3.7 percent of the amount of total undeveloped 1945-era woodland (grass) remaining in 2000. We cannot offer prognostications of future vegetation spatial structures and patterns at a landscape scale to address such a question. A spatial simulation approach, in which both development and fire are treated as a vegetation disturbance regime, could very well shed some light. However, such analysis is beyond the scope of this paper.

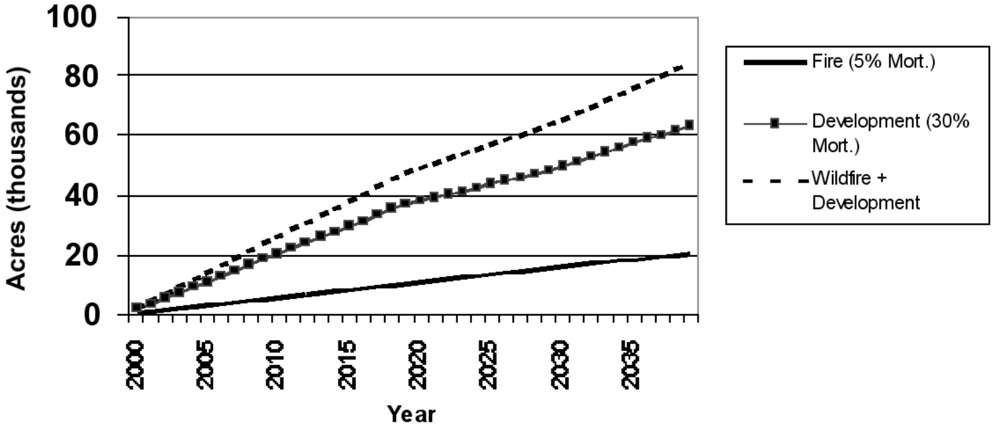

Figure 7—Potential acres of hardwood loss due to fire and development in the northwestern Sierra Nevada foothills 2000-2040.

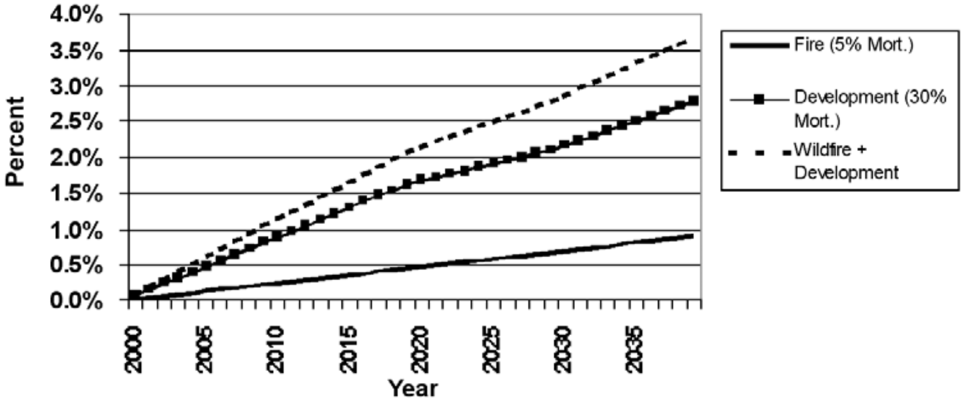

Figure 8—Potential percent hardwood loss due to fire and development in the northwestern Sierra Nevada foothills 2000-2040.

The advance of rural residential development is putting pressure on California's remaining hardwood resources, especially in the Sierra foothills. On these lands and perhaps elsewhere, development itself likely overshadows fire as an agent of impact and change within the dominant hardwood communities. These findings underscore both the need for thoughtful land development planning policies and practices at the local level, and the need to keep pace with development by meeting growing needs for fire prevention and suppression services.

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Factors Affecting the Abundance and Distribution of European Starlings at the San Joaquin Experimental Range[1]

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Abstract

We examined population trends and factors related to the abundance and presence of European starlings *(Sturnus vulgaris)* at the San Joaquin Experimental Range in the foothills of the western Sierra Nevada, 31 km east of Madera, California. Starlings first appeared there in low numbers in the late 1960s and are now abundant breeders. Simple models examining trends in starling numbers and presence/absence using point-counting data from 210 counting stations from 1985 through 2000 showed significantly increasing yearly trends in starling abundance and distribution. The yearly trend in abundance, however, became nonsignificant when weather patterns were included. Similarly, starling presence/absence showed an increasing trend over years, but the trend became sinusoidal when weather and habitat variables were included. Our data show that spurious results may occur when appropriate explanatory variables are not included in the analysis of population trends. Starlings were more abundant after years with cool summers, warm, wet winters, and on early and late count dates. Starling presence was related to habitat attributes generally considered necessary for foraging—level, open woodlands with fairly well-developed, accessible soil. Summer is the time of year when resources are most limiting for starlings in the foothill oak woodlands, as they primarily forage on arthropods in moist soils. Cool summers and wet winters permit the soils, especially swales, to remain moist and productive longer, thereby promoting higher starling abundance. Research is needed on the potential effects of starlings on native species of birds and the conservation and production values of the ecosystems they have invaded.

Introduction

The European starling (*Sturnus vulgaris*) was introduced into North America in 1890 and rapidly spread throughout most of the United States (Kessel 1953). Breeding Bird Survey data from 1968 to 1975 showed an average increase of 16 percent per year in starling numbers in the western states (Robbins and Erskine 1975). Starlings are now among the most abundant species of birds in North America, with a breeding range extending from arctic Canada to the subtropics of Mexico (Feare 1984). As populations of exotic species increase from relatively few

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individuals and a limited distribution to abundant and widespread, we expect effects on ecosystems and their component biota to increase (Hobbs and Mooney 1998).

Starlings were first documented in California in 1942 (Jewett 1942) and are now likely the most abundant bird species in the state (Small 1994). They were not documented at the San Joaquin Experimental Range (hereafter SJER), located in the foothills of Madera County, California, until the late 1960s. By 1970, SJER was home to several nesting pairs, where they nested mainly in power poles around the headquarters buildings (Duncan and others 1985). Starlings are now widespread breeders throughout SJER and the foothill oak woodlands, although they avoid ungrazed pastures (Verner and others 1997).

Cavity-nesting birds are an important and rich component of the breeding bird community in oak woodlands. Starlings are aggressive nest competitors and are known to usurp nest sites from other cavity-nesting birds (Ingold 1989, Short 1979, Troetschler 1976, Weitzel 1988, Zeleny 1978). Cavities are generally assumed to be limiting for cavity-nesting birds, and starlings use cavities similar in size and shape to those used by native species breeding at SJER, especially western bluebirds (*Sialia mexicana*) and violet-green swallows (*Tachycineta bicolor*) (Purcell 1995). Bird communities in oak woodlands are especially rich in cavity-nesting species, particularly nonexcavators that rely on cavities for nest sites that are excavated by other species (Purcell 1995, Verner and others 1997). Other than habitat loss, starlings may be the biggest threat to cavity-nesting birds in oak woodlands in California (Robbins and Erskine 1975).

Using point-count data collected at SJER since 1985, we explore trends in starling numbers and presence/absence to examine factors responsible for annual and long-term variation in starling abundance. We include weather and habitat variables to help understand the observed patterns of abundance and distribution of starlings at SJER.

Methods

Study Area

This study was done at the San Joaquin Experimental Range (SJER), in the western foothills of the Sierra Nevada, approximately 31 km northeast of Madera, California *(fig. 1)*. SJER is approximately 1,875 ha in size and ranges in elevation from 215 to 520 m. Vegetation consists of a sparse woodland overstory of blue oak (*Quercus douglasii*), interior live oak (*Q. wislizenii*), and foothill pine (*Pinus sabiniana*). The understory of scattered shrubs includes mainly wedgeleaf ceanothus (*Ceanothus cuneatus)*, chaparral whitethorn (*C. leucodermis*), hollyleaf coffeeberry (*Rhamnus ilicifolia*), and Mariposa manzanita (*Arctostaphylos viscida mariposa*). Some areas are typical blue oak woodlands, where few to no trees of other species occur, and the understory is open. Annual grasslands form a mosaic in dry areas with gentle slopes where the overstory and understory are missing. SJER has been lightly to moderately grazed since about 1900, except for a 29-ha Research Natural Area that has not been grazed since 1934.

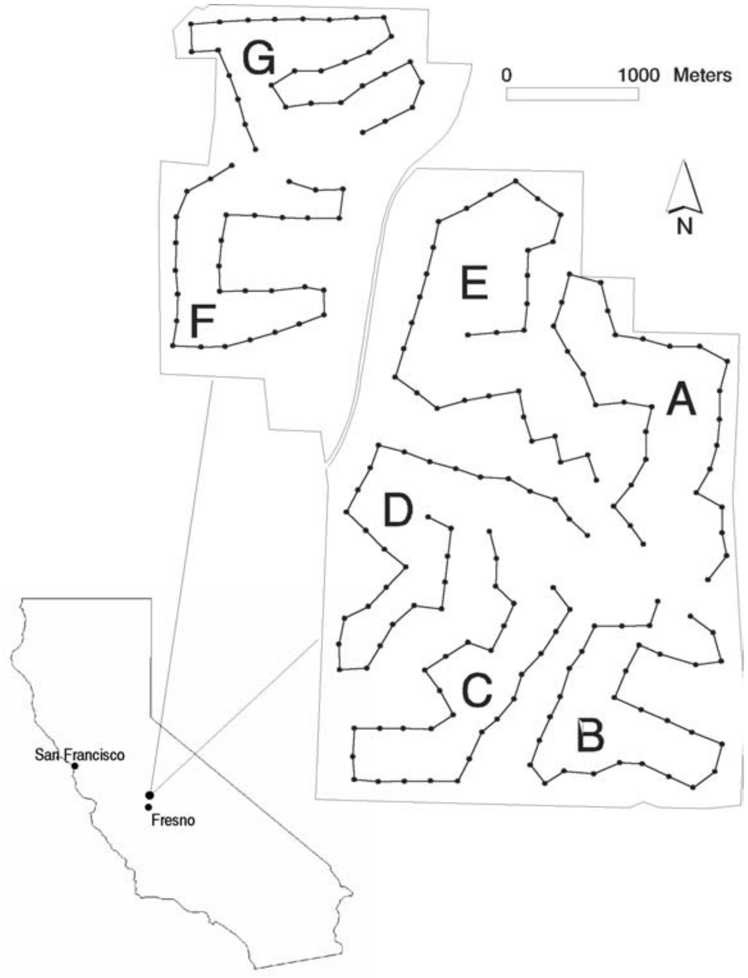


Figure 1—General location map and boundary map of the San Joaquin Experimental Range in the foothills of the Sierra Nevada, California, showing locations of point-counting stations along each of the seven sampling lines (A-G). California State Highway 41 bisects the study area just west of sampling line E.

The climate is Mediterranean, with cool, wet winters and hot, dry summers. Long-term weather records from SJER are available since 1934, showing marked yearly variations in precipitation. If we define a drought as any period ≥ 2 years in duration with ≤ 75 percent of the long-term mean annual precipitation, a drought occurred from 1987 through 1991 (Verner and Purcell 1999). This was the most prolonged and severe of the three droughts that have occurred at SJER since 1934.

Bird Counts

From three to seven observers completed 5-min, unlimited-distance point counts from 1985 through 2000. Counts were done during the peak breeding period of most species that nest at SJER, from the last week of March through the end of April. Observers were carefully selected to be proficient at bird identification, especially by songs and calls. To help minimize observer variability, a 2-week training period prior to counting helped observers sharpen their skills, and the same observers were used over as many years as possible (Verner and Milne 1989).

The sampling array consisted of 210 counting stations, with 30 stations distributed along each of seven lines established throughout SJER *(fig. 1).* Counting stations were at least 200 m apart along the same line and between the separate lines. Although this spacing is closer than ideal for independent samples, our intent was only to obtain an index of relative abundance for comparison across years. By following the same protocol each year, we believe potential biases resulting from a lack of independence in the counts are consistent from year to year. All counting stations were clearly identified by placement of yellow cattle ear tags wired to trees, shrubs, fences, and occasionally to steel fence posts, providing consistency in location across years; numerous red tags placed between stations helped guide observers from point to point along the lines.

Each year, observers were randomly assigned to lines and each observer eventually sampled all lines on seven different mornings, completing one count at each of the 210 stations. Consequently, each point was counted each year as many times as the number of observers in that year. Recording of birds at the first station on a line began at 10 minutes after official sunrise and continued at successive stations at 10-min intervals. By adhering to this schedule, each observer recorded birds at six stations per hour, with all 30 stations on a line sampled within 5 hours. Counts were not done on rainy days or when wind velocity exceeded 32 km/hr (Beaufort scale). Only results for European starlings are reported here.

We tested relations between yearly counts of starlings and nine precipitation and four temperature variables: total annual precipitation from 1 May of the year preceding the counts through 30 April of the counting year, and the 2-, 3-, 4-, and 5-year running averages of annual precipitation; winter precipitation values from October through March of the survey year, and those for 1, 2, and 3 years prior. About 86 percent of the annual precipitation falls in this period. Temperature variables included mean spring (March-May), summer (June-August), and winter (December-February) temperatures, and minimum winter temperature in the year preceding the counts. To examine the effects of the El Niño Southern Oscillation (ENSO) on starling abundance (see Sillett and others 2000), we examined five variables using annual mean monthly values of the standardized Southern Oscillation Index (SOI) to represent ENSO conditions for each calendar year. These variables included mean values for the current year, the previous year, and 2 years previous, based on the calendar year, and for April through March of the year preceding the counts and 2 years previous. High positive values of SOI indicate cold, dry La Niña conditions; low, negative values indicate warm, wet El Niño conditions (Kiladis and Diaz 1989).

Vegetation Measurements

Vegetation data were collected in 1988 at three 20-m radius plots at each of the 210 counting stations (Block 1989). Plot centers were located 40-80 m from the counting station along three axes radiating from each and separated by 120°, with the first bearing located randomly. Values for each of the three plots were averaged to describe the habitat at each station. Data from only one or two plots were available in two and 16 cases, respectively, and data from one station were missing entirely. Variables explored for inclusion in analyses were: slope (measured in degrees), aspect, distance to water, litter depth (average of 10 measures taken at 4-m intervals along the axis of the plot), grass/forb height (average of 10 measures of the grass or forb located closest to the axis at 4-m intervals), percent cover of grasses, forbs, combined grasses and forbs, foothill pine, interior live oak, and blue oak trees (based on 40 points at 1-m intervals along the plot axis). Trees were defined as woody stems >10 cm in diameter and >2 m tall. Exploratory analysis of aspect data suggested that east-facing slopes were preferred by starlings during the morning counting period. Aspect was therefore transformed to a continuous variable via

$$A' = \cos(A_{\max} - A) + 1,$$

where A is the azimuth recorded clockwise from north and A_{max} is east (90^{o}), yielding a value of 2 for east and 0 for west (Beers and others 1966).

We collected another set of vegetation measurements in 2001 that included percent cover of the three primary tree species, shrubs, and rocks within a 50-m radius centered on each counting station. Visual estimates of cover were based on assigning 2 percent cover to substrates with a 7-m radius, 1 percent for a 5-m radius, and 0.5 percent for a 3.5-m radius. For example, a tree with a crown radius of 7 m has an area of 154 m^2, or 2 percent of the 7,854 m^2 found in a 50-m radius plot. Global positioning system (GPS) northing and easting coordinates were also obtained for each counting station.

Statistical Analyses

For analysis of starling abundance, the total number of individuals detected at each point was summed over route for each observer each year. This procedure obviated any potential between-point problems of nonindependence. We used nonparametric Poisson regression models as a subclass of generalized additive models (GAM) (Hastie 1993, Venables and Ripley 1997) as a first (exploratory) statistical approach to examine relations between the number of starlings (counts) and the independent variable candidates. Explanatory variables include annual or other temperature functions, annual or other precipitation functions, sampling day (Julian date), and location (route). This approach was used in lieu of prior knowledge of the functional shapes of relations between counts and explanatory variables. We did not assume linearity. Instead the data were used to visualize the simultaneous relations between explanatory variables and counts. Generalized additive modeling was also used to drop explanatory variables that appeared to have no relation to counts. We used analysis of deviance, *F*-tests, and visual examination of the partial residual plots to select the explanatory variables to be included in the model (Hastie and Tibshirani 1990, Knapp and Preisler 1999). The exception to this rule was the independent variable *year*, which was included in all possible regression models to explore annual trends in abundance of starlings. Parametric functional shapes for the explanatory variables were obtained by trying polynomial, logarithmic, or other parametric functions suggested by the output of GAM. We used the Poisson regression model as a subclass of the generalized linear models (McCullagh and Nelder 1991) for the parametric analysis of count trends. In general, the Poisson regression model, in either nonparametric or parametric models, was as follows:

$$\log \lambda_{ijk} = \text{intercept} + f(\text{year}_i) + f(\text{julian date}_i) + f(\text{temperature}_i) + f(\text{precipitation}_i) + f(\text{SOI}_i) + \text{route}_j,$$

where

$$\text{Expected}(\text{count}_{ijk}) = \lambda_{ijk}$$

i indexes year, j indexes route, k indexes observer, f is a smoothing (Loess) or parametric function, and the count_{ijk} for each year i, each route j, and each observer k has the Poisson(λ_{ijk}) distribution. An error term (overdispersion term) was included in the model to account for the substantial variability among observers (see Verner and Milne 1989). For the parametric approach, the overdispersion term also accounted for the repeated measurement (the same observer counts birds at all the routes on different days). The GAM analysis was done with S-Plus (Mathsoft 1999) and the generalized linear models with the SAS GENMOD procedure (SAS Institute, Inc. 2000).

Because habitat data were collected at each of the 210 points, and counts at many points were zero (11 to 22 stations of the 30 per route, averaged over observers and years), we analyzed starling presence/absence at each point and for each observer instead of summing counts over routes. We again used the nonparametric generalized additive models (GAM) to model the presence/absence (odds) response, following the Logit regression model:

$$\text{Logit}(p_{ijkl}) = \log\left(\frac{p_{ijkl}}{1-p_{ijkl}}\right) = \text{intercept} + \sum_{ijk} f(\text{explanatory}_{ijk}) + \text{route}_j,$$

where p_{ijkl} is the probability of starling presence in year i, on station k of route j for the l observer, f is a smoothing (Loess) or a parametric function of the explanatory variables, and response (presence) was assumed to have an overdispersed Bernoulli(p_{ijkl}) distribution. Assuming the above Logit model, the value of p_{ijkl} is given by

$$p_{ijkl} = \frac{e^{\text{intercept}+\sum_{ijk} f(\text{explanatory}_{ijk})+\text{route}_j}}{1+e^{\text{intercept}+\sum_{ijk} f(\text{explanatory}_{ijk})+\text{route}_j}}.$$

After examining a simple model with only *year* and *route* as variables, all available variables were tried for inclusion in the habitat model, including date, time of day, and the weather variables. *Year* and the weather variables were considered due to possible relations with habitat variables, such as those related to soil moisture. Variable selection for the presence/absence response was aided by the use of classification trees (Venables and Ripley 1997). Bird-habitat relations, based on point-count data, are often weak because the habitat data describe only the general area used, not the actual location of the bird (Larson and Bock 1986). Our objective was not to produce a predictive model of starling presence, based on habitat variables, but only to see how the explanatory variables were related to starling abundance. For the presence/absence data, only the nonparametric models are presented here.

Results

Abundance (Counts)

The fitted nonparametric model including only *year* and *route* terms showed an increase in counts of starlings over the period of the study *(fig. 2a)*. The *year* effect was significant (*P*<<0.001), producing 10.2 percent drop in deviance, and the rate of change for counts was 40 percent (95 percent confidence interval was from 20 to 60 percent) from 1986 to 2000 *(fig. 2b)*. The increasing trend from 1985 through 1995 was apparently damped by the 1987 through 1991 drought, and starling numbers leveled off or decreased slightly after 1995. High variability existed among counts by individual observers, and possibly even within the same observer *(fig. 2a)*. Group foraging and flocking may also have contributed to variability in the counts. Differences among routes were especially significant (*P*<<0.001), with *route* producing a 32.3 percent drop in deviance *(fig. 2c)*.

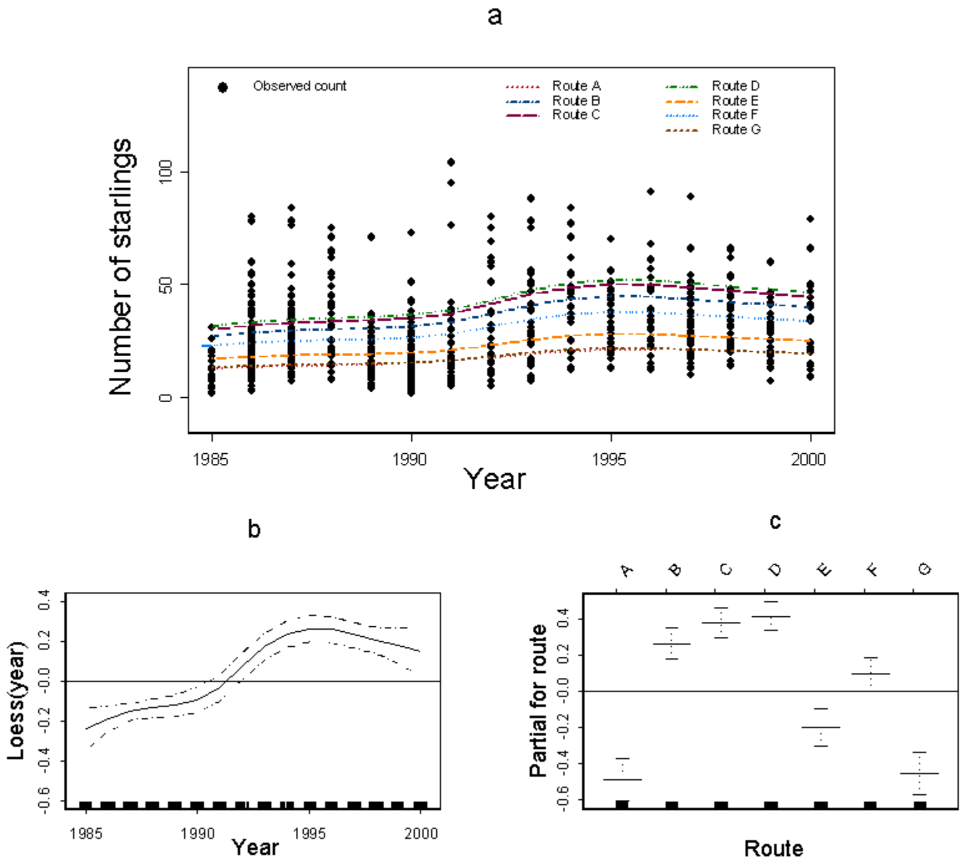


Figure 2—(a) Plot of observed counts of European starlings (*Sturnus vulgaris*) (counts per observer per route) each year (observed counts) plus the smoothed intercept (predicted counts) by route. The model is log(expected count) = loess (*year*) + *route*. (b) Plot for loess (*year*) (estimated smoothing function of *year*) showing a significant increasing trend in starling abundance. (c) Plot for estimated *route* (estimated smoothing function of *year*) effect showing significant differences among routes. The bars along the x-axis of panels b and c represent the data points.

In addition to *year*, three weather variables (*3-year running average of precipitation*, *mean summer temperature*, and *SOI*), sampling *date*, and *route* were selected with the exploratory GAM analysis to be included in the model *(fig. 3)*. Together they produced a 49 percent drop in deviance. The *SOI* variable used was the mean of the monthly indices for the 12 months from April through March immediately preceding the counts. After these variables were added to the regression, *year* became statistically nonsignificant.

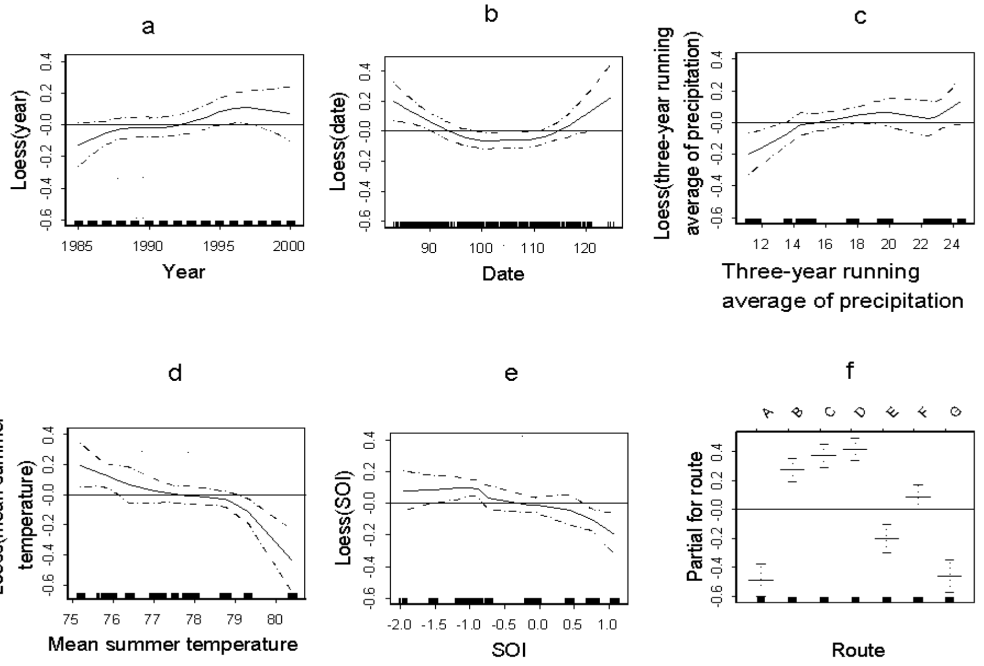


Figure 3—Plots of smoothing functions from the nonparametric Poisson model of log(expected count) estimated by GAM showing (a) nonsignificant, yearly trend in starling counts, (b) increasing counts on early and late counting dates (Julian calendar), (c) increasing counts with the *3-year running average of precipitation*, (d) decreasing counts with *mean summer temperature* (June through August), (e) the *Southern Oscillation Index* (SOI), and (f) significant differences among routes. The bars along the x-axis show the distribution of data along the axis.

Visual examination of the partial residual plots, and some trial and error, yielded the functional form for the selected explanatory variables, displayed by the following fitted parametric Poisson regression model:

$$\begin{aligned}\mathrm{Log}(\hat{\lambda}) = 390.3 - 0.007 * \mathrm{year} - 0.1582 * \mathrm{date} + 0.0008 * \mathrm{date}^2 + 0.0323 * \mathrm{pav3} \\ - 5.2441 * \mathrm{tja} + 0.7118 * \mathrm{tja}^2 - 0.0321 * \mathrm{tja}^3 \\ - 0.1304 * \mathrm{SOI} - 0.0703 * \mathrm{SOI}^2 + \mathrm{route},\end{aligned}$$

where $\hat{\lambda}$ is the estimated mean *count*, pav3 is the *3-year running average of precipitation*, and tja is *mean summer temperature*. The parametric model also showed a nonsignificant yearly trend when the other variables were present in the model *(table 1).* The other five explanatory variables were statistically significant and their patterns generally remained the same.

To summarize, *year* did not reduce the deviance significantly for either the nonparametric or parametric approach *(fig. 3a, table 1),* and the confidence interval displayed by the plot of the estimated smoothing function contained the zero line *(fig. 3a)*; the plot showed a tendency for an increasing trend. The relation between *year* and counts was stronger if the *3-year running average of precipitation* was not present in the model. Because *year* and the *3-year running average of precipitation* were highly correlated (0.63 for 1985-2000 and 0.91 for 1990-2000), the significance of both was weaker when *year* was included in both the nonparametric and parametric models. Removal of *SOI* from both models did not affect the behavior of *year* or the *3-year running average of precipitation*.

Table 1—*The full parametric Poisson regression model for starling abundance (count) showed that date, the 3-year running average of precipitation, mean summer temperature, the Southern Oscillation Index, and route were all significantly related to European starling abundance at SJER, while year was not. When the 3-year running average of precipitation was not included, year showed a significant trend.*

Independent variables	**Full model** P-value	**Without 3-year running average of precipitation** P-value
Year	0.9740	0.0002
Date	<0.0001	<0.0001
Date^2	<0.0001	0.0001
3-yr running average of precipitation	0.0982	-
Mean summer temperature	<0.0039	0.0258
Mean summer temperature^2	<0.0035	0.0299
Mean summer temperature^3	<0.0031	0.0307
Southern Oscillation Index	0.0068	0.0008
Southern Oscillation Index^2	0.1011	0.0175
Route	<0.0001	<0.0001
Model deviance	3263	3358
Null model deviance	6403	

Results from both models showed that counts of starlings were high during the early and late count dates and high on routes B, C, D, and F *(fig. 3b, f). Route* (location) produced the largest drop in deviance. Starling abundance increased with low summer temperatures in the preceding year, with a high running average of precipitation during the 3 years previous to the counting year, and with low mean monthly indices of SOI in the preceding year *(fig. 3c, d, e).* Both precipitation variables—*the 3-year running average of precipitation* and *SOI*—contributed significantly to the model and were not colinear (Pearson correlation = 0.13).

Presence/absence

The nonparametric model including only *year* and *route* terms showed a statistically significant increase in starling presence over the study period ($P < 0.000$, *fig. 4a)* and accounted for a 6.2 percent drop in deviance. The effect of the 1987 through 1991 drought on starling distribution was especially marked; this was followed by a period of increasing distribution in the succeeding wet years until 1997 when presence leveled off. Differences among routes were again highly significant ($P < 0.000$).

The weather variables appear to be modifying the behavior of the *year* effect and explaining the increasing trend in starling presence/absence. The addition of *mean summer temperature* to the model increased the drop in deviance to 6.7 percent and altered the yearly trend pattern *(fig. 4b)*. Adding the *3-year running average of precipitation* further altered the pattern to a sinusoidal curve and reduced the scale of variability *(fig. 4c)*. The best overall model, including habitat variables along with the weather variables and *year*, resulted in a 16.1 percent drop in total deviance *(table 2)*. *Year* contributed significantly to the full model, and the pattern was the same as for the model containing *year*, *route*, and the two weather variables that showed a cyclic pattern around the mean, with reduced amplitude *(fig. 4c,d)*. The variables included in the Poisson model were still important, providing confidence in their significance to starlings *(table 2, fig. 5a-c)*. For the previous analysis of count data, we could not examine *time of day*, as counts were totaled over route. In this analysis, *time of day* was significant and showed higher starling detections in the first hour of counting *(fig. 5d)*. Starlings were more frequently detected in areas that were more level than steep and that were generally east-facing, in areas with low cover of rocks, low litter depth, high blue oak cover, low live oak cover, high foothill pine cover, and low cover of shrubs *(fig. 5e-l)*.

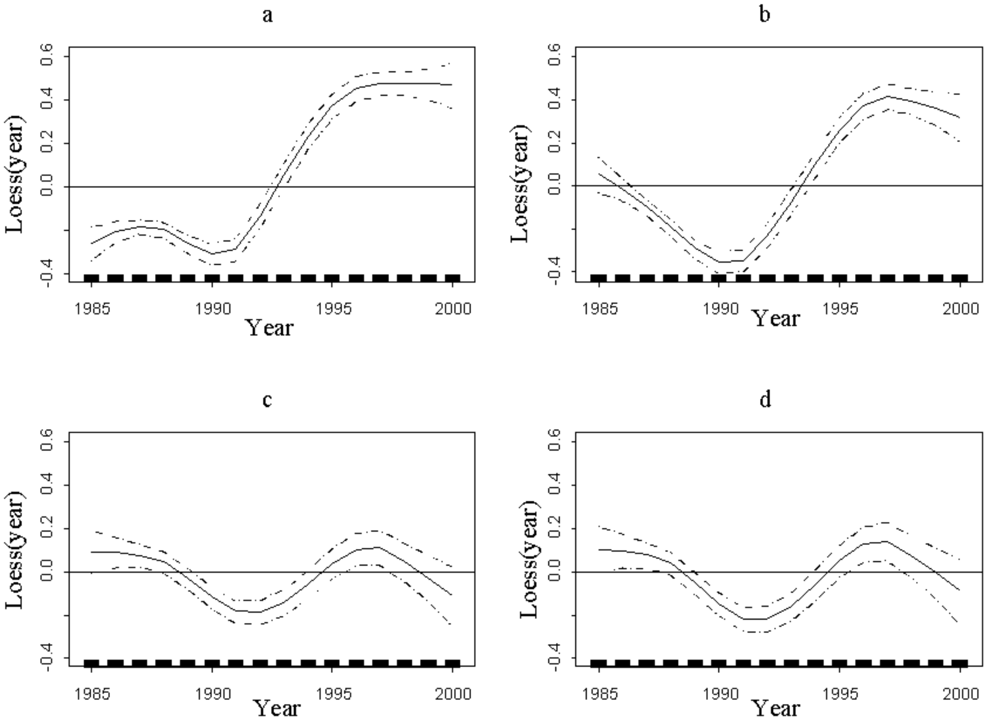


Figure 4—Plots of smoothing functions from the nonparametric logit model for starling presence/absence response (a) including only *year* and *route*, (b) *adding mean summer temperature* (June through August), (c) adding the *3-year running average of precipitation*, and (d) the full model including the habitat variables. As we add variables to the model, the year effect appeared to be driven by weather variables—both temperature and precipitation. Habitat variables did not alter the sinusoidal pattern but did contribute to the drop in model deviance. The bars along the x-axis represent the data points.

Table 2—*Analysis of deviance for independent variables in the nonparametric logit regression model examining relations between starling presence/absence and year, habitat, weather, and other variables (n = 19,019).* P-*values for the full model and all variables are < 0.0000.*

Model	Model deviance	Test deviance[1]	Pct drop in deviance
Null model[2]	18,953		
Full model[3]	19,018	4225	16.1
Full model less			
Year	22,162	67	0.1
Date	22,124	29	0.1
3-year running average of precipitation	22,127	32	0.1
Mean summer temperature	22,175	80	0.3
Route	22,168	73	0.3
Time of day	22,162	67	0.3
Slope	22,221	126	0.5
East aspect[4]	22,146	51	0.2
Pct cover of blue oak	22,212	117	0.4
Pct cover of live oak	22,165	70	0.3
Pct cover of foothill pine	22,129	34	0.1
Pct cover of shrubs	22,236	141	0.5
Pct cover of rocks	22,218	33	0.1
Litter depth	22,191	96	0.4
Easting	22,274	179	0.7
Northing	22,140	45	0.2

[1] Test deviance = (deviance of full model less one covariate) - (deviance of Full model)

[2] Null model is the model with only the intercept parameter in it.

[3] Full model is the model including the intercept parameter and all six explanatory variables.

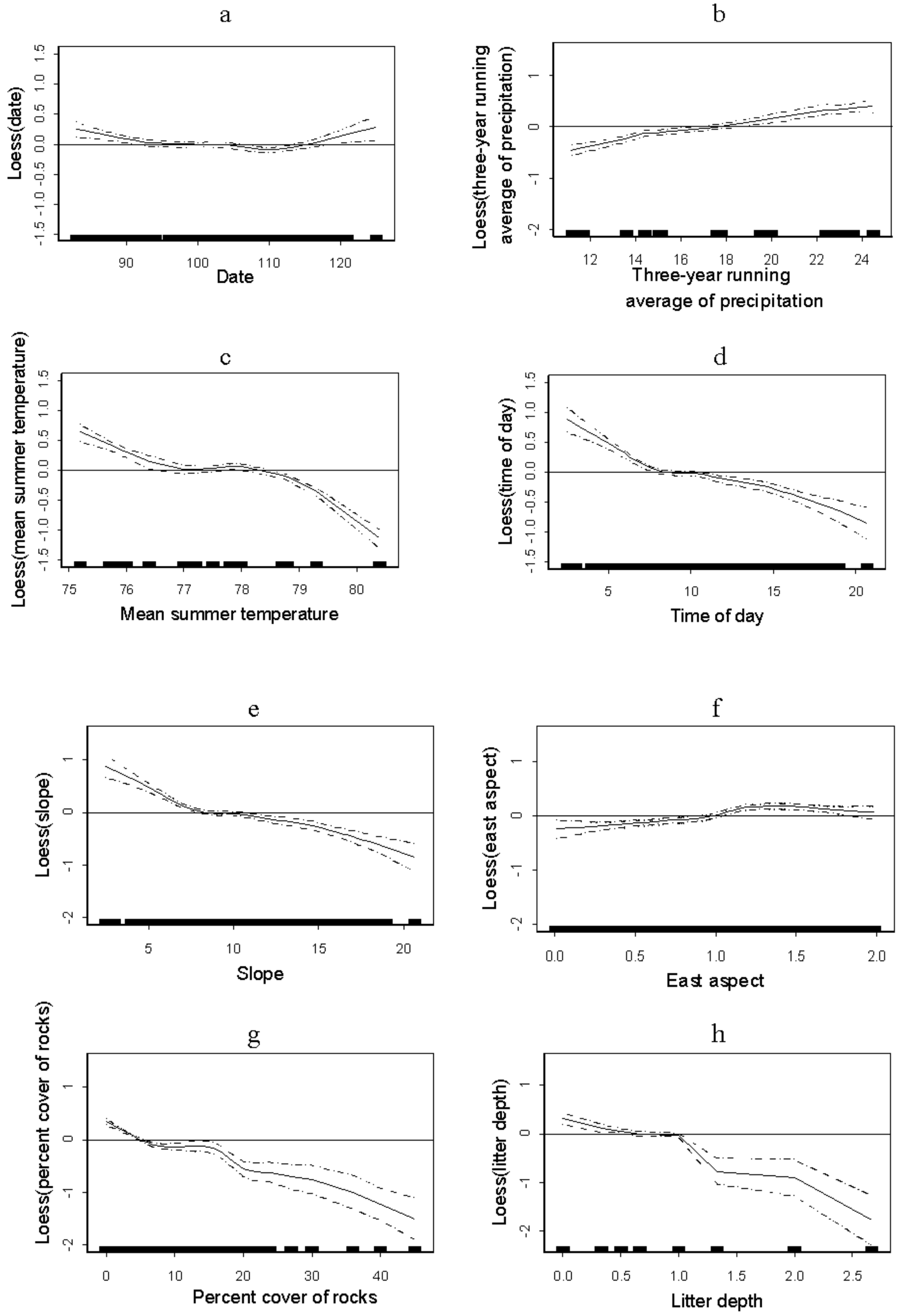
[4] Aspect is transformed to reflect east-west continuum as discussed in text.

Discussion and Conclusions

Trend in Abundance

From the first sightings in the late 1960s to becoming an abundant breeding species, starlings have clearly increased at SJER. The primary period of increase, however, occurred prior to the initiation of this study. During the period of this study, it seems that numbers of starlings follow precipitation and temperature patterns.

Our results show that simple models of population trends can give spurious results when appropriate explanatory variables are not included. Correlated variables responsible for apparent, usually short-term, increases or decreases in population numbers need to be recorded, examined, and included in models if we are to have any faith in results of trend analyses. Starling abundance and presence showed a significant increasing trend over time when *route* and *year* were the only explanatory variables *(figs. 2a, 4a),* but with the best explanatory variables present in the model, the yearly trend in starling abundance was nonsignificant.



(Figure 5 continued on next page)

(Figure 5 continued)

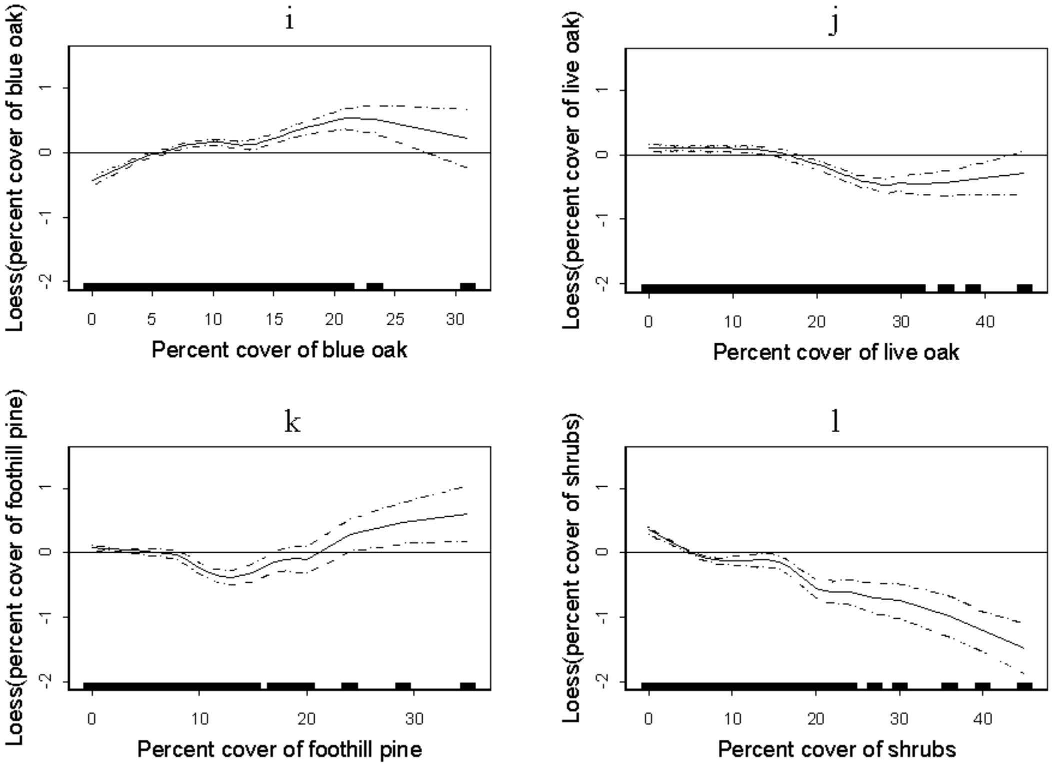


Figure 5—Plots of smoothing functions from the full nonparametric logit model for starling presence/absence response estimated by GAM, showing (a) increasing presence on early and late counting dates; (b) increasing presence with the *3-year running average of precipitation*; (c) decreasing presence with *mean summer temperature*; (d) higher detectability in the hour following sunrise; (e) decreasing presence with increasing *slope*; (f) increasing detections on east-facing slopes; (g) increasing presence with decreasing cover of rock and (h) decreasing litter depth; increasing presence with (i) increasing cover of blue oak, (j) interior live oak, and (k) foothill pine; (l) decreasing cover of shrubs. The bars along the x-axis show the distribution of data along the axis.

If multiyear rainfall patterns do, in large part, determine starling abundance at SJER, we expect that starling abundance will decrease during the next drought. The higher abundance of starlings in years after wet, warm winters and cool summers is probably indirectly related to higher productivity and resulting higher recruitment, although movement to more suitable or productive sites is also likely. The crucial question remains whether starling numbers have reached a plateau around which they will fluctuate at SJER, or whether they will continue to increase in the future.

Food resources are limiting for starlings in the summer months in Europe, where starlings are native (Feare 1985), and probably also here as described below. Arthropod numbers follow the pattern of soil moisture at SJER (Burdick and others 1989), and soil arthropods—the primary food of starlings during the breeding season (Feare 1985)—are most abundant during fall and winter, becoming scarce during the dry summer months as the ground dries and hardens and as insect larvae mature and leave the soil (Burdick and others 1989, Feare 1985). Thus, low starling abundance after hot, dry summers follows naturally. In dry years, starlings nearly disappear from SJER during July and August (K. Purcell, personal observation). Wet winters allow swales to remain moist longer into the summer months and are conducive to high starling abundance.

Habitat Relations

The predictive power of our habitat model was low due to the loose association between locations where starlings were detected and where habitat data were collected. We do, however, have some idea of the scales involved. While starlings sometimes fly long distances between roost sites and foraging locations at other times of the year, foraging locations during the breeding season are closer to nests—generally within 200 m but rarely up to 500 m (Feare 1984). While the predictive power of our model would likely improve without the spatial sampling noise in our data, we believe that the distances starlings fly are generally smaller than the scale at which we see changes in most of the habitat variables. Starlings were found in level, open habitat that had low cover of shrubs and live oaks. The suitability of level or rolling terrain is likely related to the presence of swales and their moist soils. Duncan and others (1985) reported an early observation of large flocks of starlings feeding on crane fly larvae (*Tipulidae* spp.) in swales at SJER, and preliminary data on starling foraging indicate a preference for swales (V. Wible, personal communication). Starlings appeared to avoid areas with a high density of understory—areas with shrubs and live oaks, with a shrub-like growth form. Starlings were found in areas with high cover of blue oaks. Blue oak saplings are shade intolerant, and stands of blue oaks tend to be more open than mixed stands (Verner 1988). Litter depth and rock cover were also important variables in predicting starling presence, with starlings avoiding areas with deep litter and high rock cover. These results are all consistent with the foraging needs of starlings—open, level areas with comparatively well-developed, accessible soil. Also consistent with foraging needs, starlings were found on east-facing slopes during the cool morning hours of spring where the sun would warm both the birds and their soil-dwelling prey.

Starlings have the potential to affect the diversity and resilience of the ecological community and regional biodiversity as a whole, yet we have little knowledge of factors affecting their abundance and distribution. When starlings first appeared at SJER, their distribution was local and centered around areas of human disturbance. To successfully invade oak woodlands, they had to adapt to the physical and biological conditions present. Food resources in the soil were available as long as the soil retained moisture, but to breed successfully, starlings must locate adequate food resources during the entire breeding season. Although oak woodlands may not be optimal habitat for starlings, they have nonetheless adapted to local conditions and successfully invaded these woodlands in the foothills of central California.

Future Work

Ongoing studies at SJER are investigating starling nesting and foraging ecology. One study is examining the overlap in laying dates and nest-site parameters between starlings and native cavity-nesting birds and the behavioral responses of native cavity nesters to starlings at their nests. We are also comparing soil arthropods among soil samples from starling foraging locations, random soil samples, and starling stomach samples. We continue to look for relations between starlings and their resource base. We hypothesized that starlings might avoid foraging in areas with tall grasses and forbs and high residual dry matter, such as the ungrazed Research Natural Area at SJER, because of a reduced ability to detect predators, reduced foraging efficiency, decreased maneuverability, or some combination of these factors. Our present results suggest that litter depth, not grass/forb height, explained starling occurrence and that the presence of residual dry matter is a deterrent to starling foraging. Differences in the abundance and composition of soil arthropods might also account for avoidance of ungrazed pastures. Preliminary results from our ongoing studies suggest that soil arthropods differ in abundance and species composition between ungrazed and grazed pastures. Grazed pastures were dominated by springtails (collembola), while samples from the Research Natural Area had a more balanced arthropod fauna.[4] Insectivorous birds of farmlands have been shown to prefer moderately or intensively grazed pastures (Söderström and others 2001). Morris and Thompson (1998) showed that the abundance of brown-headed cowbirds (*Molothrus ater*) was related to livestock presence and coincident high invertebrate densities, while grass height was of secondary importance. Our understanding of the starling's role in the foothill woodland ecosystem is still far from adequate. For example, we know little about their effects, if any, on the abundance and productivity of native cavity-nesting species, or about the effects of various management practices on their abundance. We do know from many studies elsewhere, however, that the addition of non-native species, compounded by habitat loss, may have significant deleterious effects on native species and the conservation and production values of ecosystems. Given the high species richness of the oak woodland avifauna, and specifically that of cavity-nesting birds (Verner and others 1997), the invasion by starlings is a real concern because of their potential for competition with native species.

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[4] Unpublished data on file, Nancy Rappaport, Pacific Southwest Research Station, Albany, Calif.

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Purple Martins in Oak Woodlands[1]

Brian D. C. Williams[2]

Abstract

Purple martins are cavity-nesting swallows that once nested fairly widely in California's oak woodlands but are now rare in that habitat. The old oaks of the Tehachapi Range (southern Sierra Nevada) may now host the last martins that nest in oak woodlands, with approximately 100-200 pairs or about 15 percent of the California population. In summer of 2000, we found 57 nests in 46 valley and blue oaks and measured over 20 variables at nest sites and random paired sites. Martins selected large-diameter trees [$\bar{x}$ = 104.3 cm diameter at breast height (dbh)] that were more prominent than random trees. Among all trees with holes, martins chose nest trees that were prominently positioned in the upper third of the landscape, and had less canopy cover at nest height than random sites. European starlings were uncommon where martins concentrated, and starlings were not observed at one area with 18 martin nests; this was the only area >1 km from any residential development. Martins may persist in portions of the Tehachapi Range because of a unique set of habitat and landscape conditions, including factors that seem to limit starlings to low densities.

Introduction

The western purple martin (*Progne subis arboricola*) (Pyle 1997) is a large, social cavity-nesting swallow that is generally rare and local in California. It is currently designated by the State of California as a Bird Species of Special Concern (Remsen 1978), and I have estimated an extrapolated statewide population of 800-1,000 breeding pairs (Williams 1998). Most of the population breeds in open coniferous forests in northwestern California, but the species is also known from oak and riparian (primarily sycamore) woodlands throughout the remainder of the state's non-desert regions (Grinnell and Miller 1944, Small 1994, Williams 1998). Oak woodlands once supported widespread populations of martins, which have been reported from oak woodlands in at least 15 counties (*table 1*) (see Williams 1998 for references), and Miller (1951) ranked oak woodlands as the second-most important habitat for this species after coastal coniferous forests. My recent distributional review (Williams 1998), however, suggests that martins persist in oak woodlands in only one or two counties. One of the state's largest martin concentrations is a remnant population in oak woodlands of the Tehachapi Range at the southern tip of the Sierra Nevada. Though I had never visited the area prior to this study, notes and discussions with locals (e.g., Grantham 1993, Hightower 1995, Moore 1998) and study of habitat maps led me to estimate that the old oaks of the Tehachapi Range may host up to 100-200 pairs, or about 15 percent of the estimated California population (Williams 1998). This population offered an opportunity to study the

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distributional ecology of martins in oak woodlands, including the influence of European starlings (*Sturnus vulgaris*) which have been widely implicated in the decline of oak woodland and other lowland martin populations since their California arrival in the 1960s (e.g., Cabe 1993, Lehman 1994, Remsen 1978, Small 1994). Specifically, my objectives were to census the nesting population in this area and evaluate nesting habitat to determine which factors best predict martin nest sites.

Table 1—*Locations where martins have nested in California oak woodlands (excluding remnant black oaks in conifer regions). A "?" indicates that nest sites were unspecified but almost certainly in oaks based on local conditions. The number of pairs is a conservative estimate, as I have indicated only 1+ pairs at many sites where "martins" (plural) were present. Regional boundaries are from Hickman (1993).*

Region	Co.	Site	Pairs	Extant	Year
Central Valley	Butte	Sacramento River, near Chico	3+	no	1903-1906
Northwestern California	Sonoma	Sebastopol?	1+	no	1870s+
Central Western California	Marin	Nicasio?	1+	no	1920's
Central Western California	Sonoma	Petaluma?	1+	no	1856+
Central Western California	Alameda	Cedar Mtn.	1+	no	1938
Central Western California	Monterey	San Antonio River	3+	no	1894+
Central Western California	Monterey	Hastings Reservation	2+	no	1942-1950+
Central Western California	Santa Clara	San Antonio Valley Rd.	1+	no	1971
Central Western California	Santa Cruz	Ben Lomond Mtn.	3+	no	1898+
Central Western California	San Luis Obispo	Paso Robles	6	no	1912+
Central Western California	San Luis Obispo	Shandon district	1+	no	1914?, -32+
Central Western California	San Luis Obispo?	Mansfield, near Nacimiento River [exact county unknown]	4+	no	1894+
Central Western California	San Benito	Paicines?	2+	no?	1899+
Central Western California	San Luis Obispo	Salinas Valley?	6+	no	1908+
Sierra Nevada	Mariposa	Yosemite Valley	1+	no	1893
Sierra Nevada	Nevada	Grass Valley	4+	no	1920s
Sierra Nevada	Tulare	Sequoia NP, foothills below	2+	no?	1930s-50s?
Southwestern California	Los Angeles	San Fernando Valley, west of	2+	no	1890's
Southwestern California	Riverside	San Jacinto, lower ridges of range	1+	no	1910's
Southwestern California	San Diego	Cuyamaca, Green Valley	1+	no?	1954
Southwestern California	San Diego	Pine Valley	1+	no	1974

(Table 1 continued)

Region	Co.	Site	Pairs	Extant	Year
Southwestern California	San Diego	Laguna Ranch	2+	no?	1894+
Southwestern California	San Diego	Julian	2+	no?	1915
Tehachapi Range	Kern	Bear Valley Springs	30+	yes	190?-1998
Tehachapi Range	Kern	Tejon Ranch	15-50	yes	1891-1986+
Tehachapi Range	Kern	Castac	3+	no?	1912

Study Area

Our study area was centered in the northern portion of the Tehachapi Range, in and near the communities of Bear Valley Springs and Stallion Springs west of Tehachapi, Kern County, California (Bear Mountain and Tejon Ranch 7.5 ft. quad maps). Two large valleys, Bear Valley and Cummings Valley, defined our eastern boundary. The western boundary was primarily the Tejon Ranch. Topography in the area is varied, but is generally hilly to mountainous and rises fairly abruptly (600-1,200 m in 1.8-3.0 km) from the southern San Joaquin Valley floor at <300 m. Two large E-W canyons, Sycamore Canyon and Chanac Creek Canyon, are roughly aligned with prevailing winds, which are regular and sometimes very strong (C. Moore, personal communication). Climate is Mediterranean with very warm, dry summers and cool, wet winters (mean annual precipitation about 38 cm), but unusual in that the oak woodlands also receive >0.6 m of annual snowfall (Western Regional Climate Center data for Tejon Rancho and Tehachapi, web address: http://www.wrcc.dri.edu/summary; Block 1989, Clendenen 2001, Moore 1998). Habitats are dominated by valley (*Quercus lobata*) and blue oak (*Q. douglasii*) woodland/savannah with a mostly naturalized grassland or shrubby understory depending on slope, aspect, and elevation. Much of the area has been or is being developed as residential parcels (roughly 1-10 acres), and intensive agriculture is dominant in Cummings Valley.

Methods

Martin Nest Surveys

We searched for martin nests from 29 June to 5 July 2000, the predicted peak of food delivery to nestlings and hence nest detection. We located active nests by scanning and listening for martins until we observed direct evidence of nesting: feeding nestlings (41/56), nestlings seen/heard (6), carrying food to hole (3), or remaining in hole as if incubating (3); the status of three other nests was unrecorded. We surveyed all habitat with potential nest cavities within the study area, namely oak woodlands and limited amounts of ponderosa pine forest (west Bear Mountain) ranging from 1,030-1,830 m. We likely found and measured >90 percent of the active nests in the study area, exclusive of one area near Bear Valley Springs (where we probably found >70 percent of nests) due to lack of time. We determined this as follows: (1) almost every bird we followed was associated with a nest, (2) our maximum martin counts were consistent with the number of known nests in an area, and (3) we did not observe any fledglings during our visits (a few nests were within 1-2 days of fledging by 5 July). We conducted surveys during all parts of the day, although martins were generally most active near the nest site in the morning hours. In addition to surveying for martins, we also noted the numbers of starlings, and the presence or absence of relatively large woodpeckers [smaller woodpeckers such as Nuttall's (*Picoides nuttallii*) and Downy Woodpeckers (*P. pubescens*) excavate cavity entrances that are typically too small for martins] and aerial foragers within or over each plot (roughly a 200-m radius—see below). We spent 0.6 - 2.0 + hrs at each plot (sometimes over two visits), sufficient to roughly characterize associations with ecologically important or indicator species (woodpeckers, swallows), or the relative abundance of starlings among areas used by martins.

Habitat Measurements

We recorded over 20 variables at 57 nests in 46 nest trees and at 38 random paired sites to analyze habitat selection (*table 2*). Data on seven additional random paired trees were recorded but not used for most analyses, as they would have constituted multiple pairs for one nest tree. We located random trees within a 200-m radius of the nest tree by a measuring two consecutive 100 m distances, with the compass direction of each 100 m each distance determined randomly (similar to Tietje and others 1997). Random tree selection excluded trees <28 cm in dbh, 8 cm smaller than the smallest nest tree reported for martins in California (Williams 1998). Random trees were not restricted to those with holes (thus potentially available for use by martins), although it would have been more meaningful for many tree- and plot-specific analyses. Similarly, we did not record variables at nonused holes, though recording such data would have been useful for studying selection of nest characteristics. We strategically avoided such measurements because doing so would have taken time from finding and measuring nest trees. As it was, the restricted duration of the study did not allow us to collect data on the remaining 11 random paired trees or additional suspected nests. All personnel were briefly trained to conduct field measurements which I occasionally checked in the field. Because visual estimates are known to be variable even among trained observers (Gotfryd and Hansell 1985), measurements at each paired site were conducted by the same observer; thus observer bias was controlled for when comparing nest sites and random sites which was the main objective of this study.

Table 2—*Selected nest, tree, and plot variables measured in this study. Additional variables recorded in the field but not analyzed in this paper are not included.*

Nest variable	Variable description
orient	Orientation of nest cavity opening, measured with a compass (degrees)
n-grd	Nest height above ground, measured with clinometer (m)
n-veg	Minimum distance from nest hole to nearest vegetation, usually visually estimated (m)
n-veghoriz	Horizontal distance from nest hole to vegetation in direction of cavity opening—a measure of the conspicuousness and accessibility of a cavity (m)

Tree variable	Variable description
tree sp.	Species of nest tree or random tree (=central tree)
dbh	Diameter at breast height (1.4 m) of the central tree (cm)
height	Height of central tree, measured with a clinometer or range finder (m)
width	Maximum canopy width of the central tree, measured through the trunk (m)
holes	Number of apparently suitable holes or cavities available for use by nesting martins, counted by scanning the tree from the ground

(Table 2 continued)

Plot variable	Variable description
rel ht 17	Height of central tree relative to other trees within a 17.8-m radius (0.1 ha): (1) tallest tree; (2) codominant; (3) within tallest 75 pct; (4) medium; (5) smallest 25 pct
prom 17	Prominence of central tree within a 17.8-m radius (0.1 ha), as determined by the maximum canopy elevation in comparison with other trees; this depends on both tree height and position in the landscape: (1) most prominent; (2) as prominent as any other tree; (3) more prominent that 75 pct of the other trees but not most prominent; (4) prominent 25-75 pct; (5) least prominent
rel ht 50	Height of central tree relative to other trees within a 50-m radius (0.785 ha): (1) tallest tree; (2) codominant; (3) within tallest 75 pct; (4) medium; (5) smallest 25 pct
prom 50	Prominence of central tree within a 50-m radius (0.785 ha), as determined by the maximum canopy elevation in comparison with other trees; this depends on both tree height and position in the landscape: (1) most prominent; (2) as prominent as any other tree; (3) more prominent that 75 pct of the other trees but not most prominent; (4) prominent 25-75 pct; (5) least prominent
No. trees	Number of trees >10 cm in dbh (minimum size used by cavity-nesting birds, Thomas and others 1979) within the 0.1-ha plot, excluding the central tree
Pct cover	Visual estimate of tree canopy cover within the 0.1-ha plot (estimates occasionally checked with densiometer): (1) <10 pct (2) 10-25 pct; (3) 25-50 pct; (4) 50-75 pct (5) >75 pct
Pct shrub	Visual estimate of shrub cover within the 0.1-ha plot: (0) 0 (1) <10 pct (2) 10-25 pct; (3) 25-50 pct; (4) 50-75 pct (5) >75 pct
Pct cover100	Visual estimate of tree canopy cover within 100 m of the central tree, estimated on a horizontal plane at nest height; or, for random trees, taken at ¾ tree height or to uppermost branch >15 cm diameter, whichever is lower: (1) <10 pct (2) 10-25 pct; (3) 25-50 pct; (4) 50-75 pct (5) >75 pct
maxdbh	Diameter of largest tree or snag within the 0.1-ha plot, excluding the central tree (cm)
slope	Slope of the 0.1-ha plot, measured with a clinometer through the central tree (0-90°)
aspect	Slope aspect of the 0.1-ha plot at the central tree (0-360°)
slp100	Relative slope position of the central tree within a circle described by a 100-m radius from the central tree (a tree on a peak is on top, a tree along a stream is usually on bottom, and a tree on the side of a long, even slope is in the middle): (1) upper 1/3, (2) middle 1/3, (3) bottom 1/3

Statistical Analysis

I used parametric and nonparametric paired-sample tests to analyze differences between variables measured at used and random sites, as it was likely that the variables were correlated by virtue of the proximity of the paired plots. Analyses of nest-specific variables were limited to descriptive statistics or chi-square (χ^2) tests. Other differences were tested using chi-square or log-likelihood chi-square for categorical variables and t-tests for continuous variables. I did not run any hypothesis tests on variables that were time-sensitive (e.g., the number of martins or starlings on a plot) since we generally spent less time at random sites vs. nest sites. A Bonferroni adjustment was used to control for experiment-wise error rates.

Results

Nests

Fifty-three of the 57 nests (93 percent) were in hollow portions of living branches that were abandoned woodpecker cavities, most of them probably from acorn woodpeckers (*Melanerpes formicivorus*). Most nests had vegetation within 0.5 m (43/57) and all had vegetation within 2.0 m. A few nests had vegetation within a meter of the entrance on a horizontal plane with the nest ($n = 5$), but this vegetation was typically sparse and/or well-spaced from other nearby vegetation; other distances were <7 m (27), 7-100 m (10), and 15 nests had completely unobstructed flight lines that extended from >100 m to as far as one could see. Nests were randomly distributed with respect to orientation (Rayleigh's $\overline{R} = 0.165$, $P = 0.217$) (Mardia 1972).

Nest Trees

Martins nested in 41 valley (50 nests) and four blue oaks (6 nests). Blue oaks were used only in the Stallion Springs portion of the study area. The species of oak for one nest was not recorded. Black oaks (*Q. kelloggii*) were not used, even though this species represented roughly 15 percent of all oaks in the study area. Nine trees had two nests and one valley oak had three nests. Nest trees were large ($\bar{x} = 104.3$ cm dbh): they averaged 16.3 cm larger than the largest tree in the plot (paired $t = 1.7$, $n = 23$, $P = 0.0949$) and were the largest diameter trees on 65 percent of the 0.1-ha plots with more than one tree. Valley oak nest trees tended to be larger than blue oak nest trees, although the relationship was not significant ($t = 0.94$, df = 39, $P = 0.353$). Martins used prominent trees, as most (35/40) were within the most prominent 75 percent of all trees within 50 m by relative height and position in the landscape. Martin nests were most often positioned on the upper third of the local slope (as measured within a 100-m radius of the nest tree) (Kolmolgorov-Smirnov $d_{max} = 22.7$, $n = 55$, $P < 0.0001$), with only two nest trees positioned on the lower third of the local slope. This relationship also applied at a larger scale as most nests were in trees positioned on the upper third of the landscape (within a 1-km radius of the nest tree)($P < 0.001$) and no nests were found on the lower third of the landscape. Of the 29 nest trees where we recorded the presence/absence of nearby woodpeckers, acorn woodpeckers were detected at 28 (97 percent), northern flickers (*Colaptes auratus*) at 13 (45 percent), and hairy woodpeckers (*Picoides villosus*) at 2 (7 percent). The most common aerial associates were violet-green swallows (*Tachycineta thalassina*) which occurred at 40 of 44 of sites where we recorded the presence of other aerial insectivores.

Nest Sites vs. Random Sites

Compared with random trees, nest trees were larger and wider (*table 3*). Holes were more than three times more numerous in nest trees (*table 3*), and only 12 of 38 of paired random trees had apparently suitable cavities. Random trees tended to be relatively shorter and less prominent in both 0.1- and 0.785-ha plots, although not significantly so (all $P > 0.10$) (*table 3*). Nest trees were more likely than random trees to occur on the upper third of a local slope (*table 3*). Overall canopy cover did not differ between nest trees and random trees, but canopy cover measured at nest height at 100 m was significantly lower at nest trees (*table 3*). Shrub cover was also lower at nest sites (P < 0.01), but it was positively correlated with canopy cover at 100 m (r = 0.41, *P* < 0.0001).

Table 3—*Descriptive statistics of continuous or categorical variables at nest sites and random sites. Paired measurements for nest variables were not taken.*

Variable	Mean	SD	*n*	min	max	Mean	SD	*n*	min	max	Test[1]	*N*[2]	*P*[3]
Nest variable													
n-grd	8.0	2.3	46	4.0	15.5								
n-veg	0.5	0.4	46	0.1	2.0								
Tree variable													
dbh	104.3	23.8	42	57	175	73.5	32.0	35	28	151	t = 4.788	31	**<0.0001**
height	15.0	3.0	46	8.5	24.0	12.6	3.7	36	6.0	20.4	t = 2.867	36	0.0070
width	16.1	4.2	45	8.6	27.6	13.6	4.2	38	5.6	23.9	T = 3.635	38	**0.0008**
holes	3.5	1.9	44	1	9	1.0	2.0	38	0	9	T_{min} = 76	34	**<0.001**
Plot variable													
rel ht 17	1.5	0.8	35	1	4	2.2	1.5	38	1	5	T_{min} = 44.5	17	>0.10
prom 17	1.7	0.9	43	1	5	2.1	1.3	27	1	5	T_{min} = 57	17	>0.30
rel ht 50	2.2	1.2	34	1	5	2.7	1.4	31	1	5	T_{min} = 52	16	>0.40
prom 50	2.5	1.0	40	1	5	3.0	1.3	22	1	5	T_{min} = 41	14	>0.50
No. trees	3.8	3.0	45	0	13	4.1	4.6	37	0	18	t = -0.118	36	0.9069
Pct cover	2.8	0.8	46	2	5	2.6	1.1	38	1	5	T_{min} = 177	29	>0.20
Pct shrub	0.3	0.6	46	0	3	1.1	1.2	35	0	4	T_{min} = 27.5	19	<0.01
Pctcover100	1.3	0.5	46	1	3	2.4	1.1	38	1	5	T_{min} = 7.5	29	**<0.001**
max dbh	82.0	31.2	25	8	140	78.5	30.3	17	26	122	t = 0.638	13	0.5354
slope	20.1	7.9	44	6	55	17.7	7.8	31	4	38	T_{min} = 185	29	>0.40
slp100	1.3	0.5	45	1	3	1.9	0.8	36	1	3	T_{min} = 15.5	20	**<0.001**

[1] Paired-sample t-tests (t), or nonparametric paired-sample Wilcoxon signed-rank test (T).

[2] Denotes number of paired samples used for the t-test, or number of paired samples excluding differences of zero for the Wilcoxon *T* test.

[3] Bonferroni adjustment for multiple comparisons requires a *P*-value of 0.0033 (0.05/15 tests) for significance at the 0.05 level or 0.0066 (0.10/15 tests) at the 0.10 level. Significant *P*-values are in bold.

Excluding random trees without holes (i.e., trees unavailable to martins), there were only two results at $P < 0.05$. The slope position of nest trees was higher (Wilcoxon $T_{min} = 0$, n = 7, $P = 0.02$), and canopy cover at 100 m was lower (Wilcoxon $T_{min} = 0$, n = 8, $P = 0.01$). Nest trees also tended to be larger than random trees with holes (121.8 ± 30.1 SD vs. 101.2 ± 17.7 SD cm dbh), but sample size was small (n = 7) and $P > 0.10$.

Starlings were uncommonly observed where martins concentrated. Starlings were not equally distributed among the three general areas where martins nested ($F = 3.92$, df = 2, $P = 0.0273$), as no starlings were observed on Black Oak Mountain – the only area >1 km from development. We did not find any starling nests in any trees we measured, partly due to the relatively late date of the study.

Discussion

Martin habitat selection appears to take place on at least four (but not mutually exclusive) levels. At the landscape level, martins may identify potential nesting areas by such factors as aerial insect availability and prevailing winds (Williams 1998), which are related to topographic position and elevation (Pedgley 1990). Elevation is also correlated with more rugged conditions and colder climates that may limit starling densities (see below).

At the broad habitat scale, martins appear to identify suitable habitat based on concentrations of suitable nest sites such as large oaks (Williams 1998) with relatively open (from above) and/or prominent positions. Martin distribution has always been patchy in California, even before starling colonization, and part of that patchiness seems to be related to the distribution of large oaks (Williams 1998).[3] This hypothesis is supported by the observation that this area has some of the largest oaks in California (e.g., see Block 1989 for comparative size; B. Williams, personal observation), especially for such relatively high elevations. In an early account of oaks and martins from near Fort Tejon in the southern Tehachapi Range, Grinnell (1905) wrote "A few western martins had nests safely ensconced in holes of lofty oaks." These oaks included "…an immense white oak, said to be the largest in California. It was 27 feet in circumference at the base, and was one of many others nearly as large.…" The relative landscape position of nest trees is also important (this study; Williams 1998). Prominent and open habitat conditions may be selected because they enhance predator detection and also allow quick and efficient access to foraging areas which are usually high.

At the nest plot or tree level, martins look for concentrations of holes in prominent and/or easily accessible substrates (Williams 1998). Martins' need of holes helps explain why they prefer large oaks, as larger trees had more holes than smaller ones (adjusted $R^2 = 0.13$, $P = 0.0002$). The number of holes, however, does not explain the total relationship with dbh. Other correlates that may help explain martin selection of large dbh trees include height and prominence: tall, prominent trees are likely to enhance predator detection and higher nests are probably less likely than lower nests to be depredated by terrestrial predators (see below). Martins, however, may simply be drawn by conspicuously large substrates.

On the nest cavity level, martins appear to prefer cavities that are easily accessible to martins and safe from predators. While some nests had vegetation within a meter of the entrance on a horizontal plane with the nest, this vegetation was usually sparse and/or well-spaced from other nearby vegetation, and martins clearly preferred unobstructed aerial pathways to visually conspicuous cavities. Nest heights averaged 8.0 m (minimum 4.0 m) above the ground, and nest height is often negatively associated with nest predation in other cavity-nesting species (e.g., Li and Martin 1991, Nilsson 1984, Rendell and Robertson 1989). Where martins nest over water (e.g., a snag with its base submerged in water), nests tend to be lower (Horvath 2000, Williams 1998), suggesting that avoidance of terrestrial predators is an important factor in nest-site selection (Horvath 2000, Williams 1998) as has been found for other cavity-nesting birds (e.g., Finch 1989, Li and Martin 1991, Nilsson 1984).

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[3] Unpublished data on file with Brian Williams, Granite Bay, California.

Considerable circumstantial evidence suggests that starlings have been a primary cause of martin declines in lowland California (summarized in Williams 1998). Starlings were abundant in Bear Valley and Cummings Valley near pastures, golf courses, parks, lawns, agricultural lands, corrals, etc., but were uncommon where we found martins, and at one area (Black Oak) with at least 18 martin nests, we saw no starlings in 3 days. The low numbers of starlings and absence of their nests may have been partly due to the relatively late date of the study, but the absence of starlings in any valley or blue oak woodland in California is unusual. Various factors may be involved here. First, only the Black Oak area was >1 km from development. Starlings were common to abundant in the urbanized valleys just 2 km to the east, but we saw no martins at Black Oak. The Black Oak area is also at 1,525 m and can be very cold during late winter and early spring (maximum snowfall occurs in March, and snow regularly occurs into April and May) when starlings usually begin nesting. Local naturalists have, in fact, observed that late (April) snows may cause starlings to abandon these high elevation oak woodlands (C. Moore, personal communication; Clendenen 2001). The high elevations of nearby Bear Valley Springs also have relatively few starlings, yet that area is residential. Another possibility may be that relatively high winds of ridgelines and canyon edges (where martin nests are concentrated) make such places energetically demanding for starlings traveling to and from foraging sites, yet favorable for the more dynamic flight behavior of martins. Much of the Black Oak area had poor-quality foraging habitat for starlings, as the area is surrounded by high canopy cover and relatively steep slopes. Furthermore, although at least part of the area is grazed by cattle, herbaceous vegetation is still relatively tall (evidenced by abundant stickers in our socks). Regardless, our observations are consistent with previous observations that starlings are generally uncommon or absent wherever martins persist. With starlings now common in most of lowland California, martins are almost exclusively found in fairly remote or rugged country (e.g., Gallagher 1997, Roberson 1993, Shuford 1993, Williams 1998). Troetschler (1976) predicted a similar distributional pattern for northern flickers as a result of competition with starlings.

Management Implications

Martins appear to persist in the Tehachapis because of a unique set of habitat and landscape conditions, including factors that seem to limit starlings to low densities. Because direct starling management (e.g., harassment, trapping) is not a practical solution (but see Weitzel 1988), martin conservation is likely to be successful only by conserving, promoting, and selecting for habitat and landscape conditions that are not only suitable for martins, but that also limit starlings. Because starlings and martins use and probably prefer similar oak woodland habitat characteristics, including nest cavity and tree conditions (multiple large holes, low canopy cover, large dbh, etc.) (Cabe 1993; see also Nilsson 1984 for habitat selection by starlings in Europe), management for martins in areas with suitable nest sites should focus on a combination of habitat (e.g., understory condition) and landscape-scale conditions (e.g., proximity to agricultural or suburban settings) that discourage starlings.

Perhaps most important, however, is the uniqueness of the oak woodlands there and their fate. The combination of large, prominent, and unusually high-elevation oaks is unique, but in most places the oaks do not appear to be replacing themselves. While regeneration is a widespread concern (e.g., Mensing 1991), the conversion of oak woodland from a wildland setting to a residential one may be problematic—and essentially irreversible. While martins themselves are relatively tolerant of both human activities and suburban or rural residential features such as pastures, lawns, and fruit trees (Brown 1997; Williams, personal observation), such human-made structures or habitats promote the invasion of starlings into oak woodlands. We observed what appeared to be a starling invasion of Stallion Springs and Bear Valley Springs, where residential conversion has started but build out is incomplete. The future of the Black Oak area is unknown, but it could be critical for Purple Martins in the northern Tehachapis. I hope this is not true, but, as their distributional history has shown, martins have not persisted well in oak woodlands.

Finally, it should be mentioned that while most historic populations are indeed extirpated, it is possible that some fairly remote oak woodlands, probably with qualities similar to those described here, are still keeping their hidden martins a secret. I would appreciate information on any of these populations.

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Cavity-nesting Bird Use of Nest Boxes in Vineyards of Central-Coast California[1]

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Abstract

Oak woodland habitat is being degraded or replaced by vineyards in many areas of central-coastal California. Oak woodlands are home to many insectivorous, cavity-nesting birds that would be beneficial in and around vineyards. During March to June 2001, we used bluebird nest boxes to study nest box use and productivity of cavity-nesting birds in vineyards versus adjacent oak woodlands. In February 2001, we placed 18 nest boxes 50 m apart in vineyards and in adjacent oak woodland at four woodland/vineyard paired sites in Santa Barbara and San Luis Obispo counties. During April to June, we visited the sites 10 times for a total of 720 nest box checks. Boxes were used by two species of cavity-nesting birds in vineyards and six species in woodlands. Nest box occupancy, clutch size, and number of nestlings were nearly equal within and outside the vineyards. This study provides preliminary evidence that nest boxes may help mitigate oak woodland habitat loss by vineyard development in central-coastal California.

Introduction

More landowners than ever are planting vineyards in central-coastal California. For example, in San Luis Obispo County the number of acres in vineyards has increased from 9,900 acres in 1996 to 26,800 acres in 2000; an average annual increase of 67 percent for each of the past four years (U.S. Department of Agriculture/ Weights and Measures 2001). In some places, this new vineyard acreage is being planted in upland areas that support oak woodlands, home to many secondary cavity-nesting birds. Many of these insectivorous bird species would be beneficial in and around vineyards. The extent to which nest boxes will attract cavity-nesting birds to vineyard sites, the species composition of the birds that use nest boxes in vineyards, and the productivity of the birds using the nest boxes compared to nearby woodland populations have not been studied.

Several studies that compared the breeding success of birds using nest boxes and cavities have demonstrated larger clutch sizes (Purcell and others 1997, Robertson and Rendell 1990), lower predation rates (Nilsson 1984, Purcell and others 1997, Robertson and Rendell 1990), and more young fledged (East and Perrins 1988, Purcell and others 1997) for some species using nest boxes. Because of such results, authors have recommended the use of nest boxes as a conservation tool to help

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[1] An abbreviated version of this paper was presented at the Fifth Symposium on Oak Woodlands: Oaks in California's Changing Landscape, October 22-25, 2001, San Diego, California.

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augment populations of cavity-nesting birds (Koenig and others 1992, Lynes 2000, Purcell and others 1997).

In this paper, we present preliminary data on nest box use and productivity of secondary cavity-nesting birds in nest boxes in vineyards and adjacent oak woodlands. Our objectives were to begin to look at the use of nest boxes in vineyards as a conservation tool to determine whether nest boxes would be compatible with vineyard management practices.

Study Area and Methods

Our study was conducted in spring 2001 in central-coastal California. Three woodland/vineyard paired study sites, each with oak woodlands adjacent to vineyards, were located in Santa Barbara County just north of Santa Ynez. The sites were approximately 10 km apart. A fourth paired site was located in San Luis Obispo County near Templeton.

The four vineyards ranged in size from 50 to 100 ha and were between 2 and 27 years old. Three of the vineyards had a fungicide or sulfur spray regimen of 7-10 day intervals that took place for 1-2 months during early summer. A dirt road separated each of the four vineyards from the adjacent oak woodlands. All four vineyards had a wire trellising system that created continuous rows of vines.

Overstory trees on the study sites were mostly coast live oak (*Quercus agrifolia)* and blue oak (*Q. douglasii)* with average density of 85 trees/ha and average diameter at breast height (DBH) of 41.4 cm. Solitary valley oaks (*Q. lobata*) were sometimes interspersed. The understory was mostly open. Woodland floors consisted primarily of annuals such as wild oats (*Avena* spp.), bromes (*Bromus* spp.) and fescues (*Festuca* spp.).

Nest boxes were constructed of 2 cm exterior plywood, had a 16 x 14 cm floor, were 27 and 39 cm tall in the front and back, respectively, and had a 3.8-cm diameter entrance hole. In February 2001, we placed 21 of the boxes (84 boxes total) in each of the four woodland/vineyard paired study sites. Boxes were placed in a 7 x 3 grid with 50-m spacing. Nine boxes were placed in a vineyard, nine boxes in adjacent oak woodland, and three boxes on the vineyard edge (*fig. 1*). Results from edge boxes are not included here. In oak woodland sites, we mounted nest boxes 2 m above ground level on live oak trees >10 cm dbh. We mounted nest boxes on t-posts (n=10), if a suitable tree was not within 5 m of a grid coordinate. Nest boxes within vineyards were bolted to 3.8-cm diameter PVC pipe and sheathed over vineyard trellis t-posts 2 m above the ground.

We determined rates of nest box occupancy and productivity by checking nest boxes each 6-10 days (10 times) from mid-April to late June of 2001. We considered the presence of an egg as evidence of nest box occupancy. Because we did not monitor nest boxes at ≤ 4-day intervals, as called for to determine nest outcome (Geupel and Hardesty 1993, Martin and others 1997), we report only the clutch size and number of nestlings that we observed in the boxes.

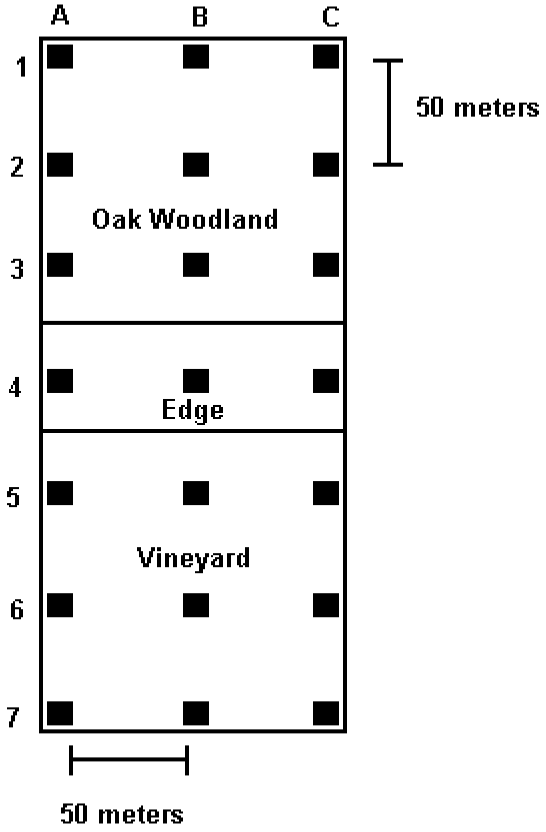

Figure 1— Nest box layout on 1 of 4 woodland/vineyard paired study plots monitored during April to June 2001 in central-coast California.

Results

Overall, nest box occupancy was 21 percent (15 of 72 boxes) (*table 1*). Occupancy was nearly equal in oak woodlands and in vineyards (19 and 22 percent, respectively). Western bluebirds (*Sialia mexicana*) and ash-throated flycatchers (*Myiarchus cinerascens*) were the most common nest box occupants, nesting in six and four boxes, respectively.

Two species nested in boxes in vineyards. Western bluebirds nested in four boxes and ash-throated flycatchers in three boxes. Average clutch size for bluebirds was 5.5 with 95 percent hatching success and 5.3 young produced per attempt. Average clutch size for ash-throated flycatchers was 4 with 92 percent hatching success and 3.7 young produced per attempt.

Six species nested in oak woodlands: western bluebirds and Bewick's wrens (*Thryomanes bewickii*) used two boxes each and ash-throated flycatchers, oak titmice (*Parus inornatus*), tree swallows (*Tachycineta bicolor*) and violet-green swallows (*Tachycineta thalassina*) each used one box. Clutch size for both bluebirds and ash-throated flycatchers was 5 with 100 percent hatching success.

Table 1—*Nest box occupancy and nesting success of secondary cavity nesting birds in vineyard (V) and oak woodland (W) study plots, central coastal California, spring 2001.*

Species	Treatment	Boxes used	Average clutch size	Average number of nestlings
Western bluebird	V	4	5.5	5.3
	W	2	5	5
Ash-throated flycatcher	V	3	4	3.7
	W	1	5	5
Bewick's wren	V	0	—	—
	W	2	6	2
Oak titmouse	V	0	—	—
	W	1	4	4
Tree swallow	V	0	—	—
	W	1	5	5
Violet-green swallow	V	0	—	—
	W	1	4	0

Discussion

Our data from one season of nest box monitoring provide preliminary evidence that at least two species of secondary cavity-nesting birds will use and produce young in vineyard nest boxes in central-coastal California. We found similar numbers of nest boxes occupied, and young produced among nest boxes placed in vineyards versus in adjacent oak woodlands. The main difference we found was in species richness with six species nesting in oak woodland boxes and two species occupying vineyard boxes. The difference in species richness may be partially due to this being the first year of this study. Purcell and others (1997) found that on their California oak-pine study site, nest box occupancy rates increased steadily from 25 percent in 1989 to 68 percent in 1994, with at least two species having low representation in the early part of the study. We expect to see increases in both the abundance and diversity of birds nesting in woodland and vineyard boxes. The diversity of birds nesting in vineyard boxes will probably never equal that of woodlands, however, because of habitat preferences not provided by vineyards.

Several factors may explain disproportionate use of nest boxes in vineyards by western bluebirds and ash-throated flycatchers. Bluebirds readily nest in boxes (Purcell and others 1997, Twedt and Henne-Kerr 2001). Bluebirds are commonly found in open habitat such as farmlands and orchards (Scott 1987). Bluebirds are also less sensitive to human disturbances than many other oak woodland species (Lynes 2000) and may have been less disturbed by management practices that occurred in the vineyards during this study. The ash-throated flycatcher, a species known to nest in a diverse range of habitats and occupy large territories is a late-arriving migrant species. This species may nest in sub-optimal locations when nest sites are limiting (Purcell and others 1997). Ash-throated flycatchers may have nested in vineyards due to a lack of available and suitable oak woodland nest sites.

Management Implications

Nest boxes could conceivably interfere with management practices such as spraying and harvesting of grapes. We found that because our vineyard nest boxes were sheathed over t-posts, the boxes did not impede normal vineyard operations during winter and spring and were easily removed after the breeding season and stored for the next nesting season so as not to interfere with the grape harvest.

Vineyard managers were also concerned with the potential of boxes attracting pest bird species that would either consume grapes or hinder vineyard operations. One common pest species, the European starling (*Sturnus vulgaris*) causes excessive economic loss on farms and usurps nest sites and possibly consumes the eggs of other bird species (Ingold 1994, Purcell and Verner 1999). We excluded starlings from our nest boxes by using an entrance hole less than 4.1 cm as advised by Giusti and Gorenzel (1993) and Lynes (2000). Another common vineyard pest is the house finch (*Carpodacus mexicanus*) which also causes economic losses to vineyard owners by consuming grapes (E. Amoral, personal communication). This bird is smaller than starlings and would have been able to use the nest boxes in this study. We did not find house finches occupying our nest boxes. Future studies should be aware, however, that vineyard nest boxes may attract this pest species which would be a negative consequence to any vineyard nest box program.

While there are some potential drawbacks to erecting bird boxes in vineyards, there are several benefits of bird boxes to vineyard managers. Though our data suggest that nest boxes in vineyards may not be used by the full suite of secondary cavity-nesting birds that occurs in oak woodlands, we found that vineyard boxes may be biologically beneficial to at least two species of secondary cavity-nesting birds, at least to the fledging stage. Bird boxes and the birds they attract are also aesthetically pleasing. Additionally, because environmental conservation is an important social topic, placing bird boxes in vineyards can serve as a valuable political tool to help enhance the conservation image of growers. Vineyard managers may therefore want to consider the inclusion of bird boxes in future vineyard management plans.

We plan to continue this study for several years and expand its scope by erecting boxes in additional vineyards in San Luis Obispo and Santa Barbara Counties.

Acknowledgments

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Effects of Residential Development and Landscape Composition on the Breeding Birds of Placer County's Foothill Oak Woodlands[1]

Diana Stralberg[2] and Brian Williams[3]

Abstract

This study examines the effect of rural residential development and landscape composition on breeding birds in Placer County's foothill oak woodlands. Point count survey data were used to construct generalized linear models for individual species' abundance or probability of occurrence, based on two sets of variables: GIS-derived landscape characteristics, including development density, oak woodland proportion, and habitat diversity; and field-collected local habitat parameters. We found that many species examined were sensitive to either development density or landscape composition at some distance between 250 and 4,000 m. Of the 48 breeding species common enough to analyze statistically, the occurrence of 24 species was significantly associated with landscape characteristics. Species shown to be associated with development density and/or urban edge proximity included the lark sparrow (-), Rufous-crowned sparrow (-), western meadowlark (-), black Phoebe (+), house finch (+) and western scrub-jay (+). Several other species were not development-sensitive but were positively associated with the proportion of oak woodland found in the surrounding landscape. For a subset of locations, some species also exhibited responses to local habitat variables, suggesting that further investigation of the importance of landscape vs. local factors is warranted. The diversity of responses observed across a range of species requires the recommendation of a multifaceted conservation strategy for oak woodland birds and their habitat.

Introduction

Placer County's human population is the fastest growing in California, with a growth rate of 3.5 percent in 2000 (California Department of Finance 2001). Much of this population growth is occurring in the county's foothill oak woodlands, 93 percent of which are privately owned and over 50 percent of which (30,000+ acres) have rural residential or urban land-use designations (Placer Legacy 2000). Concern about this rapid growth and the loss of open space and rural character led to the development of the Placer Legacy Open Space and Agricultural Conservation Program, which seeks to balance growth with the conservation of open space and wildlife resources. Because foothill oak woodlands are rapidly urbanizing and poorly protected, though treasured for their scenic and wildlife values, much of the program's early emphasis has focused on acquiring one or more large parcels to preserve oak woodlands. In addition, the County is interested in understanding how

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the rural residential landscape can be better managed to preserve wildlife, sensitive resources and water quality. This project was initiated as a part of the Placer Legacy Program as an effort to assess the effects of rural residential development and habitat fragmentation on breeding birds as indicators for oak woodland habitat.

Habitat suitability for wildlife is an important consideration in reserve design, and local habitat relationships are relatively well studied in California's foothill oak woodlands (Avery and Van Riper 1990, Block 1989, Block and Morrison 1990, Block and others 1994, Tietje and others 1997, Verner and others 1997, Wilson and others 1991). Recently, much attention has also been focused on the potential effects of rural residential development, vineyard expansion and other human modifications to oak woodland landscapes. In Sonoma County, Merenlender and others (1998) found that the level of development of a parcel influences bird community composition and that neotropical migrants in particular demonstrate reduced abundances in suburban areas and, to a lesser extent, rural residential areas. Several recent studies of birds in other California habitats have suggested that characteristics of the surrounding landscape may influence habitat quality for many species and, in some cases, may even be better predictors of species occurrence than local habitat structure (e.g., Bolger and others 1997, Stralberg 1999). Currently, a need remains for a better understanding of landscape-scale processes that affect habitat suitability of oak woodlands beyond local habitat structure (Bell 1997, Garrison and Davis 1997, Thomas 1997). Such knowledge may be particularly valuable when candidates for reserves are structurally similar, as they are in foothill oak woodlands of Placer County.

We initiated this study to test the hypothesis that some birds will be affected by landscape-scale patterns of development irrespective of local habitat. One primary objective is to provide specific recommendations to the County of Placer regarding priorities for management, conservation and acquisition of foothill oak woodlands, as well as future zoning decisions and general plan revisions. We also hope to gain a better general understanding of the features of habitat and landscape patterns that determine species occupancy, in order to inform land-use planning and conservation, as well as wildlife management on private and public land. This may be accomplished in part through future revisions to the California Partners in Flight (CPIF) Oak Woodland Bird Conservation Plan (Zack and others 2000), an interagency effort to promote the conservation of migratory birds and their habitats throughout the Americas.

Methods

Study Area

Our study area in western Placer County ranged in elevation from 70 to 480 meters, and encompassed an area of approximately 550 km^2 (*fig. 1*). Dominant tree species included blue oak (*Quercus douglasii*), which occurs primarily on drier sites (especially ridges that were historically difficult to irrigate), and interior live oak (*Quercus wislizenii*), which tends to occur in more mesic areas such as drainage basins and north-facing slopes. A complex human history has altered the distribution and structure of many of these oak woodlands, including their understory structure and composition. Interspersed with oak woodlands is a combination of orchards, cropland, dry pasture rangeland, irrigated pasture, rural residential development (“ranchettes”), and urban and suburban development.

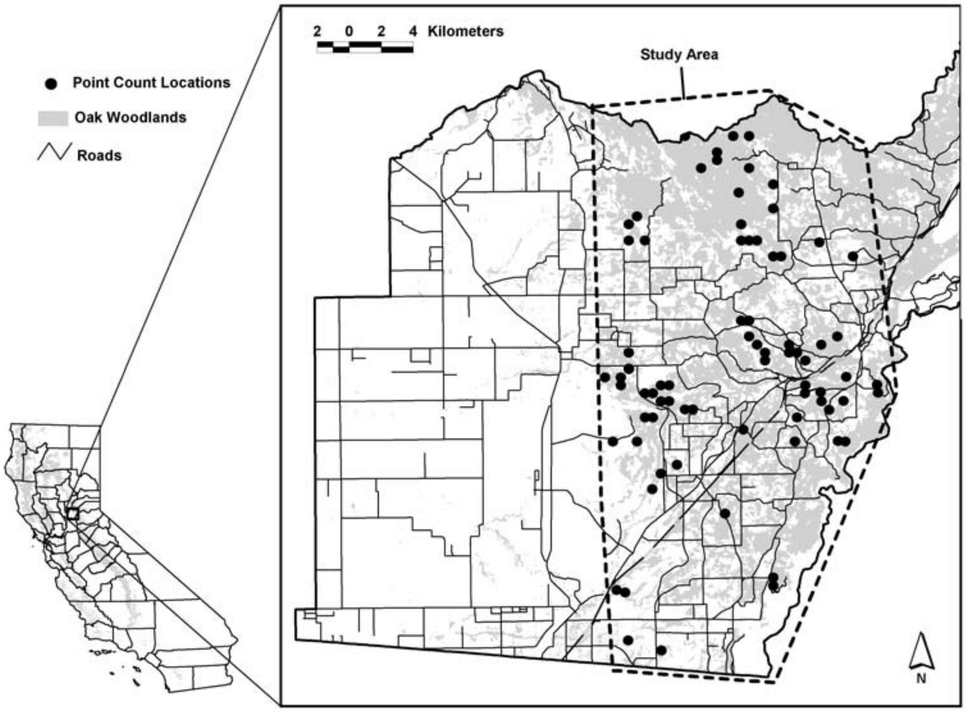

Figure 1—Study area and point count locations.

In Placer County, large intact blocks of oak woodland are rare, and habitat patches are not easily defined or necessarily isolated from other habitat patches. We therefore chose a point-based approach for sampling habitat, rather than surveying entire habitat patches. Our intent was to sample bird species at random throughout a representative cross-section of the County's development spectrum: from urban park to rural residential to largely undeveloped rangeland.

Study Design and Point Selection

A total of 75 points was surveyed. We began by selecting a stratified random sample of 80 potential survey points by generating a 500-m sampling grid of points superimposed over the county's oak woodlands within the study area. Suitable points (>2,600) were defined as meeting one of the following CWHR habitat classifications (Mayer and Laudenslayer 1988) according to GIS vegetation data (Forest Service 2000): blue oak woodland or blue oak foothill pine, but also montane hardwood, urban, annual grassland, valley-foothill riparian or agricultural cropland if our familiarity with the area suggested that the amount of oak woodland at or adjacent to the point was underestimated. Selected points were stratified by general plan land-use categories (Placer County General Plan 1994): (1) Low Density Residential (LDR) and Rural Residential (RR) 1-2.5 acres; (2) RR 2.5-5 and RR 5-10; (3) RR 10, Agricultural (Ag) 10, and Ag 20; and (4) Ag 40, Ag 80, and Open Space (OS). Actual land use varied considerably from the General Plan designation because many parcels were not yet “built out,” but this method allowed representation of a range of land uses and parcel sizes, as well as geographic area, among sample points.

To improve our sampling effectiveness, we developed a random clustering technique that began by randomly choosing one of nine 7.5 ft topographic map quadrangles followed by the random selection of a legal section (1 mi^2 or 2.59 km^2) as a starting point. We then randomly chose points from the 500-m sampling grid within immediately adjoining sections, expanding the radius by 1 section as each layer of sections was exhausted. Constraints were that no more than 4 points could fall within one section and no more than 2 points of a given land-use category could occur in any one section. This process was repeated to produce two random sets of 40 semi-clustered points, each at least 500 m from the nearest sampling point.

Because the first 80 points included no parcels zoned for 80 acres and very few parcels smaller than 5 acres, we randomly selected an additional 22 points within these parcel size ranges (10 and 12 points, respectively). Each point was ground-truthed to meet the following minimum criteria: (1) oak woodland as the dominant habitat type, with at least two oaks within the 50-m radius and a canopy cover ≥ 10 percent; (2) no house or other large building within a 50-m radius; (3) not within 500 m of a major highway; (4) not excessively time-consuming to access; and (5) <5 percent paved two-lane public road within a 50-m radius (private single-lane dirt roads were fairly common and practically impossible to exclude). We did not exclude any points based on other habitat characteristics such as presence of water, understory composition, slope or aspect.

Of these original 122 locations, we were able to obtain access to 57 survey sites. The other 45 were either unsuitable (n = 16), or we were unable to contact the landowners (n = 15), or we were denied access (n = 8), or negotiating access was too time-consuming (n = 6). We repeated the selection process to find 6 stratified-random substitute points, identified 6 points semi-randomly (randomly chosen within a non-random area that was convenient to access), and added 6 points at widely separated urban parks for which we knew we could get immediate access. Within each park, the specific sample point was randomly determined in the field. The exact location of each site was later recorded with a Global Positioning System (to within approximately 5-15 m).

Bird Counts

Six-minute, unlimited-distance point counts (Ralph and others 1993) were done twice at each of the 75 sites, 7-28 days apart (mean = 16 days, SD = 4.4). Detections were recorded as within or beyond a 50-m radius. We assumed that 2 counts would be necessary to avoid problems with seasonal variation in vocalization frequency and hence detection probability. Point counts were done in the morning beginning at official sunrise to 4 hours after sunrise, during appropriate weather conditions (Verner 1985) between 17 May and 14 June 2001 by a single expert observer (B. Williams).

Habitat Parameters

We measured or estimated parameters describing the local habitat and physical conditions at 32 of the 75 point count locations *(appendix 1)*. The intent was to statistically control for habitat-specific variation to focus on landscape-scale effects.

Landscape Parameters Obtained from GIS Data

We calculated several urbanization and landscape composition metrics *(appendix 2)* for each point-count location using ArcView 3.2a and the Spatial Analyst Extension (ESRI 2000). The County's parcel base map and associated Assessor's database were used to determine the parcel size and overall property size of each site surveyed. In addition, the number of structures within various buffer distances (250 m, 500 m, 1000 m, 2000 m and 4000 m) of each point-count location was estimated based on the development status of each parcel centroid. Because structure locations were estimated based on parcel centroids, there is some uncertainty in the number of structures counted within point count radii. Furthermore, while the bird and vegetation data were collected in 2000, the parcel base map represents July 1998 parcels and the Assessor's database contains 1999 ownership information (matching years were not available at the time of analysis). Thus, parcels that were subdivided and developed after 1998 are not correctly represented in this database. The parcel data are nevertheless a major improvement over any other available urbanization measure (i.e., Forest Service vegetation data), particularly in the rural residential zone, where the built footprint is not easily discernable even from aerial photos. As an index of housing density, we feel this measure is the best available, short of ground-based inventories.

Geographic information system (GIS) vegetation data (Forest Service 2000, 2.5 acre minimum mapping unit) were then used to coarsely determine the landcover composition of each point count location within circles of increasing radius: 250 m, 500 m, 1,000 m, 1,500 m, 2,000 m and 4,000 m. A proportion was obtained for each cover category within each radius. For analysis, the following CWHR categories were combined to calculate oak woodland coverage: blue oak woodland, blue oak-foothill pine, valley oak woodland, montane hardwood, and montane hardwood-conifer. Finer distinctions between oak woodland categories were not made due to the presumed low accuracy of the vegetation layer beyond cover class. The other category used for analysis was annual grassland, some of which was actually open oak savanna. The urban classification was not used in analysis due to the coarseness of this vegetation layer with respect to rural residential development patterns, particularly in comparison with the more accurate parcel base map and Assessor's database (*fig. 2*). To evaluate the influence of landscape-level habitat diversity, we also calculated a Shannon-Wiener diversity index (Krebs 1989) for each of the above-listed radii ($H = - \Sigma_i\ p_i \ln(p_i)$, where p_i = area of i^{th} habitat type). For this metric, each CWHR category was treated separately to reflect diversity among oak woodland as well as other habitat types.

Finally, for each point we estimated the distance to the nearest structure or urban edge, using a combination of field notes, aerial photos and the GIS parcel basemap with associated Assessor's ownership database (in that order, depending on availability). We also used 1:100,000 scale road and hydrography GIS datasets (Teale Data Center 1997, 1999) to calculate the distance from a point count to the nearest stream and nearest paved road.

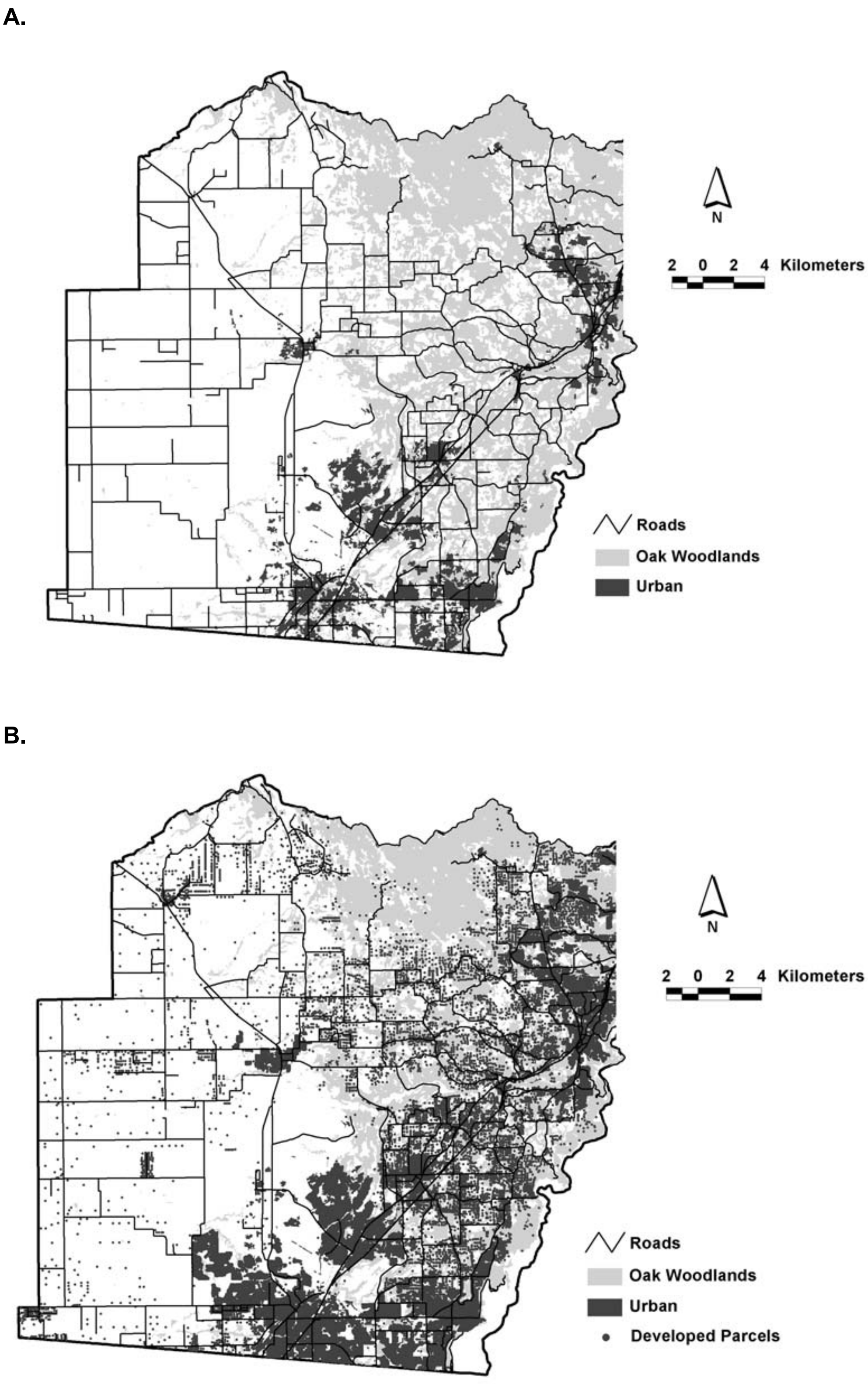

Figure 2—Differences in urban development identified by GIS vegetation data (Forest Service 2000) (a) and Placer County parcel base map and Assessor's database (Placer County 1999) (b).

Statistical Analysis

Species detected within 50 m at seven or more (10 percent) of the 75 sites throughout the sampling period were analyzed individually with respect to per point abundance or probability of occurrence. Because counts of most species had positively skewed distributions, we used generalized linear models with either a Poisson distribution and log link function or binomial distribution and logit link function (logistic regression). Poisson was the default model, but logistic regression was used for species that tended to exhibit low numbers or aggregated abundances (Hayek and Buzas 1997). Models were constructed and evaluated using Stata Version 7 (StataCorp 2000). Because many species had low detection rates within a 50-m radius *(appendix 3)* we also analyzed all detections with respect to probability of occurrence using logistic regression, statistically controlling for distance to the nearest urban edge, which at some point-count locations was within the range of bird detections (100 m or less for most species), potentially reducing the available habitat surveyed. We applied the same detection rate criterion (species occurring at 10 percent of sites or more) when analyzing all detections (unlimited distance).

To evaluate the influence of development density at various scales on bird abundance, we calculated Spearman rank correlation coefficients for each individual species and the number of structures within measurement radii of 250, 500, 1,000, 2,000 and 4,000 m. We selected landscape variables at the scales with the highest significant correlation ($P<0.05$) with bird abundance for inclusion in our initial model. Variables were included at more than one scale if graphing of correlation coefficients against measurement radius indicated more than one local maximum. We also included other landscape variables with significant Spearman correlations (distance to nearest road, distance to nearest creek or open water, elevation, parcel size and property size).

Using the subset of variables described above (pairwise correlations significant, $P<0.05$), we initially used a stepwise Poisson or logistic regression analysis (backward elimination, $P<0.15$) to select an appropriate model for each species. Variables with P-values greater than 0.05 were dropped or retained based on AIC (Akaiki's Information Criterion) comparisons with simpler models. Final models were considered significant at $P<0.01$ based on the likelihood ratio χ^2 statistic. To determine the robustness of our models, we calculated bootstrap estimates of coefficients and standard errors (200 repetitions, n=75) for each significant final model, scaling down models as necessary.

To translate results into terms meaningful to municipal planners and policymakers, we selected two development-sensitive species and calculated predicted bird abundances under existing general plan designations (as defined above).

To compare the effects of local and landscape-level variables, we constructed generalized linear models of habitat suitability for each species, using a subset of 32 sites for which local habitat variables were recorded. Again, Spearman rank correlations between species and habitat variables were used to determine significant ($P<0.05$) variables for inclusion in initial models. A stepwise regression analysis (backward elimination, $P<0.15$) using a subset of habitat variables (with models specifying the same distribution as in the analysis of landscape-level variables) was used to find the best-fitting (using AIC) significant model ($P<0.01$). Habitat models were constructed using only detections ≤ 50 m. For each significant final model, we also calculated bootstrap estimates of coefficients and standard errors (200 repetitions, n=75).

Results

Ninety-three species were detected in two visits to the 75 sites, approximately 76 of which are known or suspected to be local breeders. Limiting analysis to detections within 50 m resulted in 64 locally breeding native species. With respect to migratory status, 21 were neotropical migrants, 23 were short-distance migrants, and 22 were native residents. Nesting guilds were represented by 16 cavity nesters and 35 open cup nesters, 5 of which nest on the ground *(appendix 3).*

Landscape-Level Associations

Using generalized linear models for detections within 50 m, landscape characteristics combined explained up to 41 percent of the variation in species abundance or probability of occurrence as measured by pseudo-R^2 values (*table 1*). Species best predicted by landscape characteristics (significant bootstrap model with pseudo-R^2 greater than 0.15) were: black Phoebe, Hutton's vireo, western scrub-jay, spotted towhee, Rufous-crowned sparrow, lark sparrow, black-headed grosbeak and house finch. Development density at some scale was a significant explanatory factor for black Phoebe (+), tree swallow (-), western scrub-jay (+), Rufous-crowned sparrow (-), lark sparrow (-) and house finch (+). For tree swallow and Rufous-crowned sparrow, however, development density did not remain a significant factor in models based on bootstrap resampling trials. The violet-green swallow was positively associated with property size, while the black Phoebe and western scrub-jay were negatively associated with parcel size, but these parameters did not remain significant in bootstrap models for any species.

Table 1—*Significant (*$P < 0.01$*) regression model results for landscape-level variables (detections limited to within 50 m).*[1, 2]

Species	Model type	Pseudo-R^2	LR Chi^2	*P*	AIC	Landscape variables	Coeff.	Std.Err	*P*
BCHU	Logistic	**0.13**	**9.28**	**0.0023**	**0.85**	**GRS500**	**-6.613**	**2.690**	**0.014**
								(2.679)	(0.014)
BLPH	Logistic	**0.25**	**18.04**	**<0.0001**	**0.78**	**DEV250**	**0.188**	**0.055**	**0.001**
		(0.41)	(28.01)		(0.63)		(0.159)	(0.055)	(0.004)
						Parcel size	(-0.078)	(0.043)	(0.072)
WEKI	Poisson	(0.22)	(17.53)	(<0.0001)	(0.89)	GRS4000	(9.614)	(2.396)	(<0.001)
HUVI	Logistic	**0.18**	**11.99**	**0.0025**	**0.80**	**OAK250**	**4.306**	**2.354**	**0.067**
								(2.104)	(0.041)
						H2000	**4.457**	**2.262**	**0.049**
								(1.905)	(0.019)
TRES	Poisson	(0.28)	(13.44)	(0.0012)	(0.55)	DEV4000	(-1.5E-03)	(6.9E-04)	(0.031)
						GRS4000	(7.252)	(3.413)	(0.034)
VGSW	Poisson	(0.18)	(14.19)	(0.0008)	(1.18)	OAK4000	(4.600)	(1.555)	(0.003)
						Property size	(0.005)	(0.002)	(0.025)
CLSW	Poisson	**0.09**	**5.30**	**0.0214**	**1.62**	**GRS250**	**3.500**	**1.267**	**0.006**
		(0.25)	(36.77)	(<0.0001)	(1.52)		(2.589)	(0.736)	(<0.001)
						OAK4000	(-3.9E-0)	(1.2E-0)	(0.002)
WESJ	Poisson	**0.19**	**36.55**	**<0.0001**	**2.08**	**DEV250**	**7.1E-02**	**1.5E-02**	**<0.001**
		(0.22)	(41.90)		(2.05)		(6.4E-02)	(1.1E-02)	
						Parcel size	(-0.005)	(0.003)	(0.050)
AMRO	Logistic	**0.13**	**6.71**	**0.0096**	**0.64**	**H250**	**2.856**	**1.241**	**0.021**
								(1.210)	(0.018)
OCWA	Logistic	**0.10**	**8.66**	**0.0033**	**1.04**	**OAK4000**	**4.999**	**1.696**	**0.003**
								(2.670)	(0.008)
SPTO	Logistic	**0.27**	**21.59**	**<0.0001**	**0.86**	**OAK4000**	**6.667**	**2.461**	**0.007**
								(2.404)	(0.006)
						H2000	**7.167**	**2.459**	**0.004**
								(2.179)	(0.001)
RCSP	Logistic	**0.20**	**12.23**	**0.0005**	**0.72**	**GRS1000**	**-8.818**	**4.169**	**0.034**
		(0.36)	(22.81)	(<0.0001)	(0.64)		(-7.073)	(3.280)	(0.031)
						H4000	(6.222)	(2.704)	(0.021)
						DEV250	(-0.277)	(0.161)	(0.086)
LASP	Poisson	**0.22**	**29.57**	**<0.0001**	**1.45**	**DEV1000**	**-0.018**	**0.007**	**0.012**
								(0.006)	(0.003)
						Stream distance	**9.2E-04**	**4.7E-04**	**0.049**
								(3.4E-04)	(0.006)
BHGR	Logistic	**0.19**	**11.14**	**0.0008**	**0.69**	**Elevation**	**0.004**	**0.001**	**0.001**
									(0.004)
LAZB	Poisson	**0.12**	**14.79**	**0.0001**	**1.46**	**OAK4000**	**4.364**	**1.245**	**<0.001**
								(1.154)	
RWBL	Logistic	(0.21)	(8.87)	(0.0029)	(0.49)	Stream distance	(2.3E-03)	(8.4E-04)	(0.008)
HOFI	Logistic	**0.26**	**26.66**	**<0.0001**	**1.11**	**DEV250**	**0.162**	**0.062**	**0.009**
								(0.070)	(0.021)
						DEV4000	**4.4E-04**	**1.6E-04**	**0.007**
								(1.9E-04)	(0.023)

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[1] Bold parameter estimates and model diagnostics are based on bootstrap resampling trials. Numbers in parentheses represent parameter estimates and diagnostics from non-bootstrap models.

[2] See *appendix 2* for definitions of landscape variables and *appendix 3* for species names.

When all detections were analyzed, several additional species exhibited significant responses to landscape characteristics, with logistic regression models explaining up to 54 percent of the variation in probability of occurrence (*table 2*). In addition to the above-listed species, the presence of black-chinned hummingbird, Pacific-slope flycatcher, ash-throated flycatcher, cliff swallow, yellow-billed magpie, northern mockingbird, orange-crowned warbler and western meadowlark were reasonably well-predicted by landscape factors (pseudo-R^2 greater than 0.15 for bootstrap models). The model for chipping sparrow was strong (pseudo-$R^2 = 0.39$), but due to low detection rates for this species (8 of 75 sites), parameter estimates did not withstand bootstrap resampling validation. Controlling for urban edge distance, the species for which development density at some scale was a significant predictor of occurrence were black Phoebe (+), ash-throated flycatcher (-), western kingbird (-), tree swallow (-), cliff swallow (+), western scrub-jay (+), Rufous-crowned sparrow (-), chipping sparrow (-), lark sparrow (-), Lazuli bunting (-), western meadowlark (-) and house finch (+). For the three sparrow species, development density did not remain significant in bootstrap models, although the Rufous-crowned and lark sparrows did demonstrate an urban edge aversion (positive association with edge distance). Species demonstrating an affinity for urban edges (negative association with edge distance) were black Phoebe, house wren, and American robin, while the northern mockingbird was negatively associated with property size, a more local index of development density.

Species that were positively associated with oak woodland proportion or negatively associated with grassland proportion at one or more scales (validated by bootstrap resampling) were black-chinned hummingbird, Pacific-slope flycatcher, ash-throated flycatcher, Hutton's vireo, orange-crowned warbler, Rufous-crowned sparrow, Lazuli bunting and spotted towhee (*tables 1 and 2*). Negatively associated with oak woodland proportion or positively associated with grassland proportion (after bootstrap resampling) were western kingbird, yellow-billed magpie, cliff swallow, western scrub-jay and American crow (*tables 1 and 2*). Several species—the mourning dove, Pacific-slope flycatcher, Hutton's vireo, American robin, orange-crowned warbler, spotted towhee and Rufous-crowned sparrow—were all positively associated with habitat diversity (Shannon-Wiener H') in the surrounding landscape (after bootstrap resampling) (*tables 1 and 2*).

Finally, some species were associated with other landscape elements. Elevation was a significant predictor of yellow-billed magpie (-), house wren (-) and black-headed grosbeak (+) presence (after bootstrap resampling). Lark sparrows occurred more frequently at sites farther away from streams, while black-chinned hummingbirds and orange-crowned warblers were more likely to occur at sites closer to streams (*tables 1 and 2*).

Predicted abundances for two development-sensitive species (lark sparrow and western scrub-jay) were calculated under a range of development density scenarios (assuming constant development density) using the best model developed for each species' detections within 50m (other variables held constant at mean values). For the lark sparrow, predicted abundance (over two counts) dropped from 0.46 ± 0.23 at 40 acres per unit (Ag 40) to $7.02 \times 10^{-7} \pm 4.52$ at 1 unit per acre (RR 1.0). For the western scrub-jay, predicted abundance rose from 0.42 ± 0.20 at 40 acres per unit to 8.27 ± 0.43 at 1 unit per acre (*fig. 3*).

Table 2—*Significant (P<0.01) logistic regression model results for landscape-level variables (unlimited detections).* [1, 2]

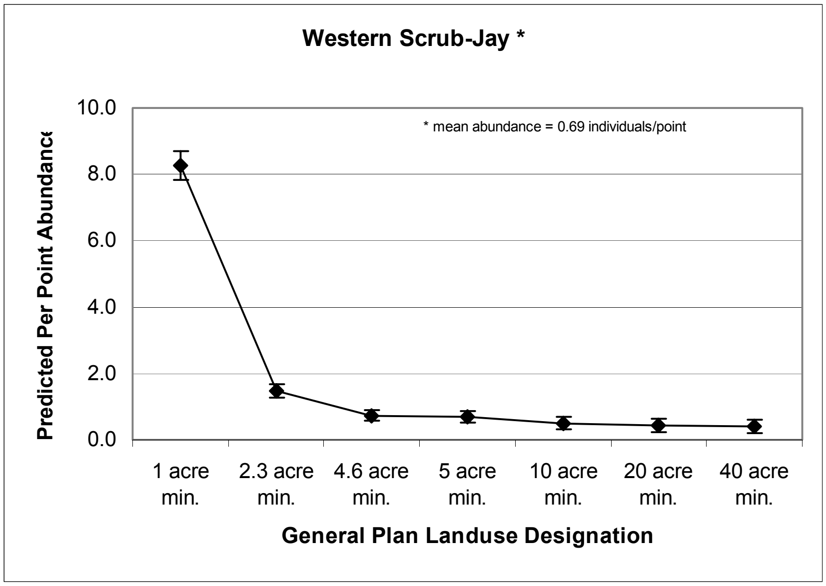
Species	Pseudo-R^2	LR Chi^2	*P*	AIC	Landscape variables	Coeff.	Std.Err	*P*
MODO	**0.13**	**12.71**	**0.0017**	**1.23**	**H250**	**-2.468**	**0.732** (0.793)	**0.001** (0.002)
BCHU	**0.23**	**15.97**	**0.0011**	**0.82**	**GRS500**	**-7.640**	**2.968** (3.688)	**0.010** (0.009)
					Stream distance	**-1.6E-03**	**8.4E-04** (8.2E-04)	**0.066** (0.060)
PSFL	**0.25**	**12.69**	**0.0018**	**0.59**	**H250**	**3.540**	**1.656** (1.346)	**0.033** (0.009)
					OAK4000	**5.665**	**3.13** (2.873)	**0.070** (0.049)
BLPH	**0.18**	**17.86**	**0.0001**	**1.18**	**DEV250**	**0.103**	**0.045** (0.055)	**0.022** (0.063)
					Edge distance	**-3.122**	**1.586** (1.954)	**0.049** (0.110)
ATFL	**0.27**	**24.73**	**0.0001**	**1.00**	**DEV500**	**-0.096**	**0.039** (0.031)	**0.013** (0.002)
					OAK500	**4.410**	**1.647** (1.603)	**0.007** (0.006)
					DEV1000	**0.012**	**0.007** (0.005)	**0.062** (0.013)
WEKI	**0.14**	**11.90**	**0.0026**	**0.99**	**DEV250**	**-0.118**	**0.067** (0.078)	**0.077** (0.128)
					GRS250	**3.306**	**1.590** (1.306)	**0.037** (0.011)
HUVI	**0.16**	**13.53**	**0.0012**	**1.03**	**OAK250**	**4.221**	**1.349** (1.696)	**0.002** (0.013)
					H4000	**3.458**	**2.297** (1.923)	**0.132** (0.072)
TRES	**0.14** (0.23)	**9.47** (14.93)	**0.0021** (0.0006)	**0.81** (0.76)	**DEV4000**	**-8.1E-04** (-1.3E-03)	**4.2E-04** (4.5E-04)	**0.043** (0.011)
					OAK4000	(-4.981)	(2.238)	(0.026)
CLSW	**0.26**	**18.61**	**0.0001**	**0.79**	**DEV4000**	**3.7E-04**	**1.9E-04** (1.5E-04)	**0.053** (0.011)
					GRS250	**3.520**	**1.603** (1.400)	**0.028** (0.012)
WESJ	**0.21**	**19.67**	**0.0001**	**1.09**	**DEV500**	**0.059**	**0.030** (0.020)	**0.049** (0.003)
					OAK500	**-3.536**	**1.981** (1.469)	**0.074** (0.016)
YBMA	**0.20**	**15.38**	**0.0005**	**0.88**	**GRS500**	**3.570**	**1.907** (1.796)	**0.061** (0.047)
					Elevation	**-2.3E-03**	**1.2E-03**	**0.068** (0.060)
AMCR	0.16	14.71	0.0006	1.09	GRS1000	(4.209)	(1.940)	(0.030)
					Edge distance	(-6.572)	(2.639)	(0.013)

***Table 2** (cont.)*

Species	Pseudo-R^2	LR Chi^2	*P*	AIC	Landscape variables	Coeff.	Std.Err	*P*
HOWR	**0.13**	**13.63**	**0.0011**	**1.25**	**Elevation**	**-2.1E-03**	**8.9E-04** (8.3E-04)	**0.018** (0.012)
					Edge distance	**-3.363**	**1.684** (1.588)	**0.046** (0.034)
AMRO	**0.07**	**7.11**	**0.0077**	**1.31**	**Edge distance**	**-3.012**	**1.608** (1.388)	**0.061** (0.030)
NOMO	**0.27**	**24.20**	**<0.0001**	**1.07**	**Property size**	**-0.031**	**0.012** (0.011)	**0.008** (0.006)
OCWA	**0.33** (0.39)	**32.79** (38.60)	**<0.0001**	**0.98** (0.93)	**OAK4000**	**8.939** (13.364)	**3.124** (3.702)	**0.004** (<0.0001)
					H4000	**7.049** (6.964)	**2.773** (2.979)	**0.011** (0.019)
					Stream distance	**-1.6E-03** (-1.4E-03)	**8.8E-04** (6.8E-04)	**0.078** (0.033)
					Edge distance	(-3.273)	(1.462)	(0.025)
SPTO	**0.26**	**24.81**	**<0.0001**	**1.04**	**GRS500**	**-5.949**	**2.126** (2.149)	**0.005** (0.006)
					H2000	**4.965**	**1.980** (1.752)	**0.012** (0.005)
RCSP	**0.23** (0.28)	**17.88** (22.01)	**0.0001** (<0.0001)	**0.88** (0.85)	**H2000**	**4.499** (4.582)	**2.367** (1.709)	**0.057** (0.007)
					Edge distance	**4.108** (4.499)	**2.673** (1.707)	**0.124** (0.040)
					DEV250	(-0.222)	(0.149)	(0.136)
CHSP	(0.39)	(20.01)	(0.0002)	(0.54)	DEV250	(-0.926)	(0.543)	(0.088)
					H500	(-3.438)	(1.730)	(0.047)
					Elevation	(0.003)	(0.001)	(0.045)
LASP	**0.23** (0.28)	**22.74** (27.39)	**<0.0001**	**1.07**	**Stream distance**	**1.3E-03** (1.50E-03)	**6.2E-04** (5.8E-04)	**0.036** (0.010)
					Edge distance	**4.521** (2.839)	**2.280** (1.467)	**0.0547** (0.053)
					DEV250	(-0.178)	(0.099)	(0.072)
BHGR	**0.08** (0.12)	**7.63** (11.49)	**0.0058** (0.0032)	**1.24** (1.22)	**GRS1000**	**-4.185** (-5.790)	**1.824** (2.079)	**0.022** (0.005)
					Edge distance	(-2.002)	(1.080)	(0.064)
RWBL	(0.12)	(10.10)	(0.0064)	(1.11)	Stream distance	(1.4E-03)	(5.3E-03)	(0.008)
					Edge distance	(-2.388)	(1.413)	(0.091)
WEME	**0.26** (0.52)	**21.10** (42.01)	**<0.0001**	**0.84** (0.59)	**DEV2000**	**-0.007** (-0.015)	**0.002** (0.006)	**0.005** (0.017)
					GRS250	(9.017)	(2.946)	(0.002)
HOFI	**0.12**	**11.93**	**0.0026**	**1.19**	**DEV4000**	**5.5E-04**	**2.0E-04** (2.2E-04)	**0.007** (0.010)

[1] Bold parameter estimates and model diagnostics are based on bootstrap resampling trials. Numbers in parentheses represent parameter estimates and diagnostics from non-bootstrap models.

[2] See *appendix 2* for definitions of landscape variables and *appendix 3* for species names.



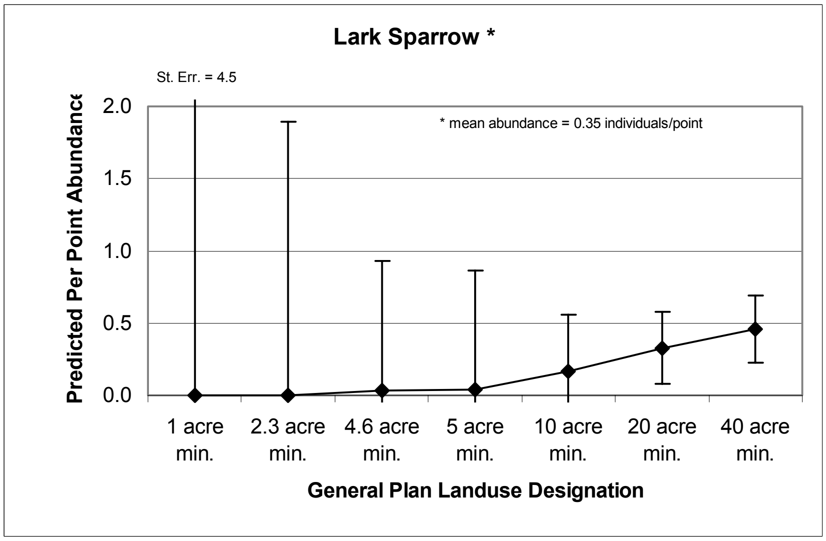


Figure 3—Predicted effects of housing density (by general plan land-use designation) on development-sensitive species.

Local Habitat Associations

Model results suggest that the occurrences of many species are significantly predicted by one or more habitat parameters (*table 3*). Due to low sample sizes, however, most of the final models were not sufficiently robust, as indicated by bootstrap resampling simulations. Species that were well-predicted by habitat variables (with bootstrap models significant at $P<0.01$) were, in order of model explanatory power (pseudo-R^2), western scrub-jay, orange-crowned warbler, Bewick's wren and brown-headed cowbird. Each of these species was predicted by different local habitat variables.

Table 3—*Significant (*P *< 0.01) regression model results for local habitat variables (detections limited to within 50 m).*[1, 2]

Species	Model type	Pseudo-R^2	LR Chi^2	P	AIC	Habitat variables	Coeff.	Std.Err	P
BCHU	Logistic	(0.34)	(13.03)	(0.0003)	(0.91)	# QW	(0.022)	(0.008)	(0.004)
ACWO	Poisson	(0.52)	(53.90)	(<0.0001)	(1.77)	Granary Tree	(3.581)	(0.578)	(<0.001)
						# QL	(0.202)	(0.057)	(<0.001)
NUWO	Poisson	(0.22)	(11.68)	(0.0029)	(1.50)	# QK	(-0.911)	(0.415)	(0.028)
						Grazing Level	(0.991)	(0.326)	(0.002)
HUVI	Logistic	(0.44)	(14.59)	(0.0007)	(0.79)	Percent Slope	(0.074)	(0.047)	(0.113)
						# QK	(1.113)	(0.498)	(0.025)
CLSW	Poisson	(0.49)	(26.65)	(<0.0001)	(1.06)	# QL	(0.182)	(0.061)	(0.003)
						Freq. Human Visits	(2.018)	(0.765)	(0.008)
WESJ	Poisson	**0.42** (0.52)	**41.03** (50.04)	**<0.0001** (<0.0001)	**1.93** (1.71)	**# QL**	**0.159** (0.139)	**0.053** (0.032)	**0.003** (<0.001)
						# Trees	**-0.011** (-0.014)	**0.004** (0.005)	**0.013** (0.009)
						Habitat Edge	(0.525)	(0.890)	(0.005)
BUSH	Logistic	(0.19)	(7.25)	(0.0071)	(1.09)	# QD	(0.059)	(0.033)	(0.071)
BEWR	Logistic	**0.14** (0.42)	**10.64** (15.88)	**0.0011** (0.0012)	**2.49** (1.09)	**Avg. Height**	**-0.293** (-0.599)	**0.097** (0.329)	**0.002** (0.069)
						# Snags	(1.020)	(0.576)	(0.069)
						Grazing Level	(-1.722)	(1.148)	(0.133)
HOWR	Logistic	(0.54)	(10.71)	(0.0011)	(0.41)	QW Canopy	(0.147)	(0.082)	(0.074)
WEBL	Poisson	(0.73)	(35.81)	(<0.0001)	(0.54)	Avg. dbh	(0.296)	(0.069)	(<0.001)
EUST	Logistic	(0.67)	(23.68)	(<0.0001)	(0.57)	# Trees	(-0.044)	(0.021)	(0.039)
						Max. dbh	(0.120)	(0.053)	(0.024)
OCWA	Logistic	**0.25** (0.34)	**10.91** (14.55)	**0.0010** (0.0007)	**1.14** (1.08)	**QW Canopy**	**0.058** (0.051)	**0.026** (0.022)	**0.024** (0.022)
						Avg. dbh	(-0.172)	(0.105)	(0.103)
SPTO	Logistic	(0.37)	(15.44)	(0.0004)	(0.99)	Avg. dbh	(-0.268)	(0.128)	(0.036)
						# Snags	(0.850)	(0.417)	(0.042)
CALT	Poisson	(0.48)	(6.96)	(0.0083)	(0.42)	Avg. Height	(-1.075)	(0.510)	(0.035)
BRBL	Poisson	(0.44)	(18.68)	(<0.0001)	(0.87)	# Trees	(-0.077)	(0.033)	(0.020)
BHCO	Poisson	**0.14** (0.32)	**8.12** (18.76)	**0.0044** (<0.0001)	**1.72** (1.45)	**# QK**	**0.514** (0.500)	**0.175** (0.177)	**0.003** (0.005)
						Rock Outcrop	(-1.055)	(0.380)	(0.006)
BUOR	Logistic	(0.49)	(9.74)	(0.0018)	(0.44)	Avg. dbh	(0.333)	(0.170)	(0.050)

[1] Bold parameter estimates and model diagnostics are based on bootstrap resampling trials. Numbers in parentheses represent parameter estimates and diagnostics from non-bootstrap models.

[2] See *appendix 1* for definitions of local habitat variables and *appendix 3* for species names.

Landscape and habitat associations are summarized in *table 4* for species with best-fitting landscape-level models (Pseudo-R^2 > 0.20) in addition to focal species included in the Oak Woodland Bird Conservation Plan (Zack and others 2000).

Table 4—*Summary of landscape and habitat associations for species with best-fitting landscape models and CPIF focal species.* [1][2]

Species	CPIF focal species status	Frequency (50 m / all)	Landscape model R^2 (50 m / all) (pct)	Development response[3]	Landscape oak woodland response[4]	Habitat model R^2 (50 m) (pct)	Positive habitat correlates	Negative habitat correlates
CAQU	2°	0.07 / 0.37						
BCHU		0.17 / 0.17	0 / 23		**positive**	34	# QW	
ACWO	1°	0.29 / 0.73				52	granary trees, # QL	
NUWO	2°	0.27 / 0.63				22	grazing level	# QK
PSFL		0.07 / 0.11	- / 25		**positive**			
BLPH		0.19 / 0.39	41 / 18	**positive**				
ATFL	2°	0.36 / 0.71	0 / 27	**negative**	**positive**			
WEKI		0.08 / 0.23	22 / 14	**negative**	**negative**			
HUVI	2°	0.16 / 0.25	18 / 16		**positive**	44	# QK, percent slope	
TRES		0.08 / 0.16	28 / 23	**negative**	positive			
CLSW		0.13 / 0.19	25 / 26	**positive**	**negative**	49	freq. human visits, No. QL	
WESJ	1°	0.39 / 0.67	22 / 21	**positive**	**negative**	52	**# QL*,** habitat edge	**# trees***
YBMA	1°	0.05 / 0.20	- / 20		**negative**			
OATI	1°	0.93 / 0.99						
WBNU	2°	0.48 / 0.73						
BEWR	2°	0.47 / 0.67				42	snags	**avg. height*,** grazing level
BGGN	1°	0.01 / 0.05				0		
WEBL	1°	0.11 / 0.20				73	avg. dbh	
NOMO		0.09 / 0.44	- / 27	**positive**				
EUST	2°	0.41 / 0.53				67	max. dbh	# trees
OCWA		0.24 / 0.36	10 / 39		**positive**	34	**QW canopy***	avg. dbh
SPTO		0.23 / 0.35	27 / 26		**positive**	37	snags	avg. dbh
CALT	2°	0.12 / 0.40				48	none	avg. height
RCSP		0.15 / 0.21	36 / 28	**negative**	**positive**			
LASP	1°	0.17 / 0.35	22 / 28	**negative**		0		
CHSP		0.04 / 0.11	- / 39	negative	positive			
WEME		0.01 / 0.23	- / 52	**negative**	negative			

[1] Refer to *tables 1-3* for model details. R^2 values are Pseudo-R^2 values from Poisson or logistic regression analysis (non-bootstrap). Bold type indicates variables and species with robust bootstrap resampling results.

[2] See *appendix 1* for definitions of local habitat variables and *appendix 3* for species names.

[3] As measured by development density, parcel size, property size or edge distance.

[4] As measured by oak woodland proportion within any measurement radius.

Discussion

Although the limited sampling of local habitat parameters reduced the robustness of our models, our data suggested fairly strong relationships between the occurrence and/or abundance of several bird species and local habitat variables. Clearly, local habitat characteristics directly influence a species' ability to feed, avoid predators and reproduce. Larger landscape characteristics may not be important for a songbird that meets all of its survival, feeding and reproduction goals within a small area, as long as the local habitat within its home range is suitable. This may especially be true in a landscape such as the Placer County foothills, where habitat fragmentation has generally not progressed to the stage of discrete, isolated oak woodland fragments (*sensu* Wiens 1994). Thus one would not predict that gradual extirpation of small populations from isolated habitat fragments (*sensu* MacArthur and Wilson 1967) would be an important process in this area.

Nevertheless, some of the species detected in our study did exhibit significant responses to characteristics of the surrounding landscape. Lark sparrow and Rufous-crowned sparrow abundances were negatively associated with development density, as was the occurrence of ash-throated flycatcher, western kingbird, tree swallow and western meadowlark. Conversely, the western scrub-jay, house finch and other species were positively associated with development density. This suggests that residential development in the oak woodland landscape may indirectly affect some bird species outside the area of immediate impact.

Urbanization-associated declines in bird abundance may be regulated by a variety of mechanisms, including increased urban-associated nest predators, anthropogenic habitat degradation, urban edge avoidance, increased dispersal mortality, and indirect responses to elimination of top-level predators (potentially resulting in the mesopredator release hypothesized by Soulé and others 1988). Ground-foraging birds such as lark, chipping and Rufous-crowned sparrows, may be particularly vulnerable to domestic cat *(Felis catus*) predation, as well as to ground-level disturbances such as mowing and grazing, which may limit seed availability.

With respect to nest predation, one might suspect that the higher presence of western scrub-jays, an important nest predator for many songbird species (Geupel and DeSante 1990), in more developed landscapes, could have detrimental effects on the reproductive success of other songbirds. Further demographic study would be needed to detect these effects.

Other species such as the Orange-crowned warbler, Hutton's vireo, Pacific-slope flycatcher and spotted towhee appear to respond to landscape composition and landscape-level habitat diversity but not necessarily to the presence of development *per se*. For these species, the amount, configuration and diversity of available oak woodland habitat in the surrounding landscape seems more important than the number of built structures. Although we were unable to control for local habitat conditions in our landscape models (due to small sample sizes), we did not find local habitat parameters to be strongly correlated with landscape composition. Thus we suspect that landscape-level fragmentation of oak woodland habitat, whether natural or human-induced, may affect populations of several bird species independent of local habitat conditions.

Variations in life history strategies probably make some species more susceptible than others to habitat fragmentation (Hansen and Urban 1992). Species with large foraging ranges, short dispersal distances, or widely-dispersed populations may depend on landscapes with higher proportions of suitable habitat (oak woodland in this case). In addition, some neotropical migrants may respond to larger landscape patterns (Hansen and Urban 1992), although several researchers have argued that traditional fragmentation paradigms based on eastern U.S. studies may not apply in the western U.S., where wooded habitats tend to be naturally fragmented (Verner and Larson 1989, Tewksbury and others 1998). Our results, though preliminary, support the notion that migratory species may be more susceptible to changes in the amount and configuration of oak woodland habitat configuration. Of the eight species that were positively associated with the proportion of oak woodland habitat in the surrounding landscape (after bootstrap validation), all but the Rufous-crowned sparrow and possibly spotted towhee are short-distance or neotropical migrants.

Comparisons with Other Studies

For many of the species detected, our results are consistent with previous similar studies. The negative association between Rufous-crowned sparrow abundance and development density, as well as urban edge distance, is consistent with the results of two southern California scrub studies (Bolger and others 1997 and Stralberg 1999), which also found negative landscape-level associations with urbanization for this species. Rufous-crowned sparrows tend to be patchily-distributed in our study area, as they are generally restricted to grassy slopes with scattered boulders and/or shrubs. While this species is capable of colonizing successional habitats (Shuford 1993, Williams, personal observation), its dispersal ability through unsuitable habitats may be limited.

Results for other resident species generally correspond with those of similar studies, which also found positive urbanization associations for northern mockingbird (Bolger and others 1997, Stralberg 1999), house finch (Bolger and others 1997, Merenlender and others 1998) and western scrub-jay (Merenlender and others 1998). Other resident species for which we found no significant development associations, including Bewick’s wren, California quail, California towhee and bushtit, are more scrub- than woodland-associated and often occupy shrubby habitats within residential areas (Blair 1996). In scrub habitat, neither Bolger and others (1997) nor Stralberg (1999) found significant urbanization associations for any of these species.

Among short-distance migrants, the lark sparrow and western meadowlark responded to both development density and landscape-level habitat composition (with lark sparrow preferring oak woodland and western meadowlark preferring grassland/oak savanna-dominated landscapes). These species were also found by Bolger and others (1997) to be edge/fragmentation sensitive. For the lark sparrow, Breeding Bird Atlases in Sonoma and Monterey Counties provide anecdotal evidence that the species is no longer found in apparently suitable habitat near urban areas where it was formerly present (Humple 1999).

Caveats

With respect to GIS data sources, the vegetation layer (Forest Service 2000) used to calculate landscape composition and habitat diversity was fairly coarse (2.5 acre minimum). It was thought to overestimate oak woodland types, misidentifying non-native ornamental trees as oaks or classifying open oak savanna as grassland. Furthermore, landscape metrics calculated at large scales, particularly at the 4000 m radius, may reflect physical gradients unrelated to urbanization or landscape composition *per se.*

We are also cautious about interpreting local habitat relationships as they were based on a small subset of sites that was not randomly selected. Although they do represent the extreme ends of the development spectrum (urban parks and large undeveloped parcels), some portions of our study area are underrepresented, primarily those that contain smaller rural residential parcels. Habitat models for most of the species examined were not robust enough to withstand bootstrap resampling simulations. Thus some of the habitat relationships we found may have been spurious, and deserve further examination with a more complete dataset.

Furthermore, the results presented here are based on a single year of data. High levels of background variability in point count surveys found by other researchers in similar habitat (Verner and others 1996) suggest that additional years of data are needed to validate our models. Additional data would also increase detection rates, allowing more robust analyses of seemingly development-sensitive species with low detection rates (e.g., chipping sparrow).

Finally, as with any study that attempts to relate point count survey results with habitat or landscape characteristics, we must caution that adult abundance (or presence) is not necessarily an indication of habitat quality. Many areas may function as population sinks, drawing in birds from healthy populations elsewhere, yet failing to replace the population with new recruits (Brawn and Robinson 1996, Donovan and others 1995). To fully assess the relationship of rural residential development and habitat fragmentation on breeding birds, data on reproductive success and adult survival are needed.

Implications for Conservation Planning

Our results highlight the fact that the importance of local habitat and landscape characteristics may vary greatly by species. On one end of the response spectrum, several sparrow species appear to experience negative consequences of human development. Our models predict that lark sparrow densities would be reduced (below the mean detected in this study) at development densities greater than 5 acres per parcel, and would be virtually non-existent (albeit with large error bounds) at a one acre per parcel density (*fig. 5*). Although we lack information on sustainable densities for these species (but see Zack and others 2000), low densities predicted by our models are of concern. Further study over multiple years would be necessary to identify population trends.

For other woodland species, including orange-crowned warbler and Hutton’s vireo, the quality, the amount and configuration of available habitat in the surrounding landscape seem more important than the number of built structures. This suggests that development that retains oak woodlands (including a significant interior live oak component within the blue oak matrix) may still provide adequate habitat for these species. Other species such as Bewick’s Wren appear insensitive to development and landscape characteristics but are well-predicted by the presence of certain local habitat features.

Conserving habitat for birds across this development-sensitivity spectrum is no easy task, and may hinge upon several complementary strategies:

- Preserving the remaining large, undeveloped parcels of oak woodland (>40 acres) should help ensure the local persistence of landscape-sensitive species.
- Limiting the subdivision of rural residential parcels into small (1-5 acre) ranchettes may help sustain development-sensitive species in more marginal areas.
- Managing oak woodlands on small parcels to retain a variety of habitat components including large trees, snags and interior live oaks can provide habitat for a host of human-tolerant avian species.
- Oak woodland species have varying habitat needs, so maintaining a mosaic of habitat types is important for preserving a suite of oak woodland species.

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Appendix 1—*Descriptions of local habitat variables measured (or estimated) at each survey location for the area within a 50 m radius.*

Variable	Description	Variable	Description
Percent slope	Percent slope of point	Avg. height	Average height of canopy (m)
Aspect	Slope aspect of point	Max. height	Height of tallest tree (m)
# QD	Number of blue oaks >2" dbh	Shrub cover	Shrub cover category (0-5)
# QW	Number of live oaks >2" dbh	Bare soil	Amount of exposed soil (0-3)
# QL	Number of valley oaks >2" dbh	Grass height	Herbaceous layer height category (1-4)
# QK	Number of black oaks >2" dbh	Grass density	Herbaceous layer density category (0-3)
# PS	Number of gray pines >2" dbh	Grazing intensity	Grazing intensity (0-3)
# PP	Number of ponderosa pines >2" dbh	Rock outcrops	Rock outcrop amount (0-4)
Trees	Number of total trees >2" dbh	Granary tree	Number of Acorn Woodpecker granary trees
Snags	Number of snags >5" dbh	Down wood	Estimated number of pieces of downed wood >10cm in diameter and ≥1m in length
Canopy cover	Percent tree canopy cover	Freq. human visits	Estimated level of human visitation during breeding season (0-4)
QW canopy	Percent live oak canopy cover	Habitat edge	Presence of obvious ecotone
Avg. dbh	Average dbh of all trees	Grazing level	Estimated level of grazing intensity (0-3)
Max. dbh	Diameter of largest tree		

Appendix 2—*Descriptions of landscape-level variables measured for each survey location.*

Variable	Abbreviations	Description
Development density	DEV250, DEV500, DEV1000, DEV2000, DEV4000	Number of human-built structures within 250 m-4000 m radius circle, as estimated by development status of parcel centroids
Oak woodland proportion	OAK250, OAK500, OAK1000, OAK2000, OAK4000	Percent of 250 m-4000 m radius circle containing oak woodland habitat, including blue oak woodland, blue oak-foothill pine, valley oak, montane hardwood and montane hardwood-conifer
Grassland proportion	GRS250, GRS500, GRS1000, GRS2000, GRS4000	Percent of 250 m-4000 m radius circle containing annual grassland, including some oak savanna
Habitat diversity	H250, H500, H1000, H2000, H4000	Shannon-Wiener diversity index ($H = -\Sigma_i p_i \ln(p_i)$, where p_i = area of i^{th} habitat type) within 250 m-4000 m radius circle
Elevation		Elevation (m) of point count location based on 30 m digital elevation model (USGS)
Stream distance		Distance (m) to nearest stream based on 1:100K hydrography GIS layer (Teale Data Center)
Road distance		Distance (m) to nearest road based on 1:100K road GIS layer (Teale Data Center)
Edge distance		Distance (m) to nearest human structure based on a combination of field notes, parcel base map and digital aerial photos

Appendix 3—*Summary of bird species detected at 75 sites visited twice during the breeding season (excluding waterfowl, shorebirds and raptors).*[1]

Common name	Latin name	AOU Code	No. of sites detected (≤50 m)	No. of sites detected (unlimited)	Breeding status	Migratory status
Ring-neck pheasant	*Phasianus colchicus*	RPHE	4	30	B	R
Wild turkey	*Meleagris gallopavo*	WITU	4	11	B	R
California quail	*Callipepla californica*	CAQU	5	28	B	R
Mourning dove	*Zenaida macroura*	MODO	20	46	B	R
Black swift	*Cypseloides niger*	BLSW	1	2	?	NTM
Black-chinned hummingbird	*Archilochus alexandri*	BCHU	13	13	B	NTM
Anna's hummingbird	*Calypte anna*	ANHU	32	34	B	SDM
Calliope hummingbird	*Stellula calliope*	CAHU	1	1	?	NTM
Acorn woodpecker	*Melanerpes formicivorus*	ACWO	22	55	B	R
Nuttall's woodpecker	*Picoides nuttallii*	NUWO	20	47	B	R
Downy woodpecker	*Picoides pubescens*	DOWO	4	4	B	R
Hairy woodpecker	*Picoides villosus*	HAWO	1	2	B	R
Western wood-pewee	*Contopus sordidulus*	WEWP	3	12	B	NTM
Willow flycatcher	*Empidonax traillii*	WIFL	3	3	NB	N/A
Hammond's flycatcher	*Empidonax hammondii*	HAFL	1	1	NB	N/A
Dusky flycatcher	*Empidonax oberholseri*	DUFL	1	1	NB	N/A
Pacific slope flycatcher	*Empidonax difficilis*	PSFL	5	8	B	NTM
Black Phoebe	*Sayornis nigricans*	BLPH	14	29	B	R-SDM
Ash-throated flycatcher	*Myiarchus cinerascens*	ATFL	27	53	B	NTM
Western kingbird	*Tyrannus verticalis*	WEKI	6	16	B	NTM
Hutton's vireo	*Vireo huttoni*	HUVI	12	19	B	NTM
Warbling vireo	*Vireo gilvus*	WAVI	5	8	NB	NTM
Tree swallow	*Tachycineta bicolor*	TRES	6	12	B	NTM
Violet-green swallow	*Tachycineta thalassina*	VGSW	10	13	B	NTM

Appendix 3 (cont.)

Common name	Latin name	AOU code	No. of sites detected (≤50 m)	No. of sites detected (unlimited)	Breeding status	Migratory status
Cliff swallow	*Petrochelidon pyrrhonota*	CLSW	10	14	B	NTM
Barn swallow	*Hirundo rustica*	BASW	2	3	B	NTM
Western scrub-jay	*Aphelocoma californica*	WESJ	29	50	B	R
Yellow-billed magpie	*Pica nuttalli*	YBMA	4	15	B	R
American crow	*Corvus brachyrhynchos*	AMCR	4	22	B	R-SDM
Oak titmouse	*Baeolophus inornatus*	OATI	70	74	B	R
Bushtit	*Psaltriparus minimus*	BUSH	48	57	B	R
White-breasted nuthatch	*Sitta carolinensis*	WBNU	36	55	B	R
Bewick's wren	*Thryomanes bewickii*	BEWR	35	50	B	R
House wren	*Troglodytes aedon*	HOWR	6	31	B	SDM-NTM
Blue-gray gnatcatcher	*Polioptila caerulea*	BGGN	1	4	B	SDM-NTM
Western bluebird	*Sialia mexicana*	WEBL	8	14	B	R-SDM
Swainson's thrush	*Catharus ustulatus*	SWTH	1	2	NB	N/A
American robin	*Turdus migratorius*	AMRO	8	31	B	SDM
Wrentit	*Chamaea fasciata*	WREN	4	11	B	R
Northern mockingbird	*Mimus polyglottos*	NOMO	7	33	B	R
European starling	*Sturnus vulgaris*	EUST	31	40	B	R
Cedar waxwing	*Bombycilla cedrorum*	CEWA	1	3	NB	N/A
Orange-crowned warbler	*Vermivora celata*	OCWA	18	27	B	SDM-NTM
Yellow warbler	*Dendroica petechia*	YWAR	5	7	?	NTM
Yellow-rumped warbler	*Dendroica coronata*	AUWA	1	2	NB	N/A
Black-throated Gray warbler	*Dendroica nigrescens*	BTYW	1	1	NB	N/A
Townsend's warbler	*Dendroica townsendi*	TOWA	2	4	NB	N/A
Wilson's warbler	*Wilsonia pusilla*	WIWA	7	9	NB	N/A
Yellow-breasted chat	*Icteria virens*	YBCH	1	7	B	NTM
Western tanager	*Piranga ludoviciana*	WETA	4	8	NB	N/A

Appendix 3 (cont.)

Common name	Latin name	AOU code	No. of sites detected (≤50 m)	No. of sites detected (unlimited)	Breeding status	Migratory status
Spotted towhee	*Pipilo maculates*	SPTO	17	26	B	R-SDM
California towhee	*Pipilo crissalis*	CALT	9	30	B	R
Rufous-crowned sparrow	*Aimophila ruficeps*	RCSP	11	15	B	R
Chipping sparrow	*Spizella passerina*	CHSP	3	8	B	SDM-NTM
Lark sparrow	*Chondestes grammacus*	LASP	13	26	B	SDM
Song sparrow	*Melospiza melodia*	SOSP	3	8	B	SDM
Black-headed grosbeak	*Pheucticus melanocephalus*	BHGR	10	25	B	NTM
Lazuli bunting	*Passerina amoena*	LAZB	18	29	B	NTM
Western meadowlark	*Sturnella neglecta*	WEME	1	17	B	SDM
Red-winged blackbird	*Agelaius phoeniceus*	RWBL	6	20	B	R-SDM
Brewer's blackbird	*Euphagus cyanocephalus*	BRBL	7	15	B	SDM
Brown-headed cowbird	*Molothrus ater*	BHCO	25	36	B	SDM-NTM
Bullock's oriole	*Icterus bullockii*	BUOR	9	17	B	NTM
Hooded oriole	*Icterus cucullatus*	HOOR	1	2	B	NTM
House finch	*Carpodacus mexicanus*	HOFI	35	49	B	SDM
Lesser goldfinch	*Carduelis psaltria*	LEGO	52	61	B	SDM
Lawrence's goldfinch	*Carduelis lawrencei*	LAGO	3	2	B	SDM
American goldfinch	*Carduelis tristis*	AMGO	15	21	B	SDM
House sparrow	*Passer domesticus*	HOSP	3	10	B	R

[1] B = Breeding, NB = Not Breeding, NTM = Neotropical Migrant, SDM = Short-distance Migrant, R=Resident

To Prune or Not to Prune: Responses of Coast Live Oaks (*Quercus agrifolia*) to Canopy Retention during Transplanting[1]

Rosi Dagit[2] and A. James Downer[3]

Abstract

A total of 62 coast live oaks (*Quercus agrifolia*) were monitored since they were initially boxed for transplantation in 1993. At that time, only branches injured during the moving process and deadwood were removed, leaving the entire canopy intact. This was a departure from the usual transplanting methodology that traditionally removes up to 70 percent of the canopy in order to compensate for the massive root loss incurred during boxing. To date, survival of non-pruned trees has exceeded that of a cohort of 25 transplanted oaks that received the standard canopy reduction. A discussion of the impacts of pruning and transplanting on diameter growth, canopy condition and overall health and vigor of the transplanted oak trees is provided.

Introduction

Transplantation of mature coast live oak (*Quercus agrifolia*) as mitigation for development of oak woodlands has been a common practice in southern California. Typically, tree canopies are severely pruned (up to 70 percent loss) at the time of root pruning, which usually takes place in the extreme heat of late summer/early fall. The justification for this is to reduce transpirational stress and "balance" the root:shoot ratio.

Since 1992, the City of Calabasas, California, has required monitoring of 4 development sites where coast live oaks were transplanted as part of a mitigation effort to compensate for the loss of oak woodland resources to development. At Sites 1-3, a total of 30 mature coast live oaks with severe root and canopy pruning were monitored following boxing in January 1992 to October 1997. At Site 4, only the roots of 100 mature coast live oaks were pruned, leaving the canopies intact, except for removal of deadwood and any branches damaged during the moving process. Monitoring of the 4th site began in October 1996 and concluded in April 2001.

Comparing the condition and survival rate of the trees that retained their natural canopies to the severely pruned trees provides important data on the effects of extensive canopy loss on mature transplanted coast live oaks. To date, few studies have evaluated the success of transplanting mature coast live oaks, the physiological

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responses of the trees to the extensive root loss, or the cost effectiveness of moving trees considering the need for long-term maintenance and poor survival rates. Roberts and Smith (1980) did a 1-year-study of water potential and stomatal conductance of oak trees impacted by root injury from trenching and found that mortality increased when more than half of the root system was impacted. Scott and Pratini (1992) followed the health and vigor of 593 transplanted coast live oaks in Orange County, California, for more than 4 years and found that following high initial mortality, trees that began to decline were unable to regain lost vigor and subsequently died. Dagit and Downer (1996) reported on the survival status of the 30 pruned trees at Sites 1-3, finding that 16 percent of the trees died immediately following boxing. Of those that survived the initial trauma, 28 percent of the trees were dead, 24 percent were nearly dead, 32 percent were in decline and only 16 percent were stable 5 years after transplanting.

This study compares canopy recovery, leaf tissue conditions, growth and condition of the pruned to the non-pruned transplanted coast live oak trees.

Transplantation Methodology

All portions of the sites from which trees were moved experienced extensive grading and drainage changes before replanting. Sites 1, 2 and 4 were originally north-facing hillside drainages with intermittent streams, clay soil, and mixed chaparral/oak woodland vegetation. Following grading, the sites consisted of 95 percent compacted cut and fill pads which maximized development opportunities. Site 3 was initially a level riparian area that was transformed into a freeway interchange, with limited area for planting.

Trees were selected for transplanting by the developer's tree-moving company and their arborists. Trees selected ranged in size from 15 to 175 cm DBH and most were multi-stemmed. Tree height ranged from 4-15 meters. Crown diameter varied as well, from 4 to 25 meters. Concurrent with root pruning and side boxing, the canopies of the selected trees were pruned at Sites 1-3, removing up to 70 percent of foliage bearing branches. Deadwood, nearly all inner foliage, and many terminal buds were trimmed, leaving a thin shell of foliage on the perimeter of the canopy. At Site 4, the tree canopy was left intact, with only dead branches or damaged branches removed *(fig. 1)*.

A backhoe was used to trench all four sides around each tree, resulting in the loss of approximately 90 percent of the root system. Plywood box sizes ranged from 1.5 to 8.5 meters wide, and 1 to 2.5 meters deep. Bottom boxing was completed 3 to 6 months later. After boxing, trees were irrigated weekly by water trucks, as directed by the tree-moving company. The trees were planted in a hole dug by backhoe, usually 1 to 2 meters wider than the box and approximately the same depth as the root ball. The plywood box bottoms were left in place, the sides removed, and backfilling done by backhoe and hand tools. Sprinklers were installed at Sites 2 and 4, and irrigation was automated and poorly overseen. The other two sites continued to be watered by truck one to three times weekly. By coincidence, 3 of the trees were planted in the same orientation as they had originally grown.

The situation at Site 4 is unusual, in that 31 trees have been planted, while the remainder are still boxed. A wildfire swept through the property in October 1996, burning many of the boxed trees, but none of the planted trees. The 31 burned, boxed trees were thus removed from further consideration in this study. Despite inoculation with mycorrhizae, mulching and irrigation, these boxed trees continue to decline. Those planted in the landscape have been subjected to a variety of irrigation and drainage problems.

The majority of the transplants have been installed in common open space areas, except at Site 4, where they have also been placed on private property, adjacent to driveways and street intersections.

Pruned coast live oak

1993
Original condition

After pruning

2001
Present condition

Non-pruned coast live oak

1996

2001

Figure 1—Photographs of pruned and non-pruned transplanted coast live oaks (trees rated as stable).

Monitoring

The monitoring protocol included quantitative and qualitative observations of both transplanted and control trees on a quarterly, then on a semi-annual basis. At each site, one to eight control trees were selected from undisturbed areas on the development parcel having soil type, orientation, slope conditions, and sizes comparable to the transplanted trees. Unfortunately, several of the control trees have subsequently been impacted by adjacent landscaping changes, and are showing signs of decline. Every time the trees were observed, each tree was given a vigor rating from 1 (dead) to 5 (excellent). The rating was modified from the International Society of Arboriculture standard condition evaluation for landscape trees that includes evaluation of canopy, foliage, trunk, and root condition *(table 1)*.

Table 1—*Vigor rating scale.*

Vigor rating	Description	Criteria for evaluation
1	Dead	No living canopy
2	Decline	Less than 50 percent living canopy, few growth cracks (<1mm), some root and trunk defects, moderate pest infestation or disease.
3	Stable	50 percent or more living canopy, few growth cracks (1-3 mm), some root or trunk defects, minor infestation or disease
4	Good	Greater than 75 percent living canopy, many growth cracks (1-4 mm), few root or trunk defects, minimal pest infestation or disease
5	Excellent	Well balanced, symmetrical canopy, many growth cracks (1-8 mm), few root or trunk defects, healthy tree.

Diameter at breast height (4.5 feet above grade) was measured quarterly, along with visual estimation of canopy density. Data concerning size and number of growth cracks indicating new growth in the trunk and branches were also collected.

Each spring, shoot length, number of leaves and number of shoots per terminal bud were measured from five randomly selected samples within reach of the ground on each tree. Presence of insect pests, diseases, flowers and acorns were also recorded. Leaf tissue samples were collected once a year from four cardinal points within reach around the lower canopy, and sent to the lab for analysis.

Soil probing to examine roots down to a 30 cm depth started one meter from the trunk of both control and transplanted trees. Probes were also done at mid-canopy, at the dripline, at the perimeter of root ball, just outside the box edge, and 1.5 meters farther out. Samples were qualitatively examined in the field, noting presence, size (mm), and density of roots (number per cm). At Sites 2 and 4 in October 1997, non-woody root samples (less than 5 mm width, 5 cm length) were taken from the top 15cm of soil at four cardinal points around the mid-dripline of the trees and plated to identify any infection by *Armillaria* sp. and *Phytophthora* sp. Additionally, in May 2001 at Site 4, root samples were collected at four cardinal points within the dripline using a soil probe. Root fragments were sorted from the soil sample to determine root length and dry weight. Soil volume was determined for each sample. All non-pruned trees were inoculated with ectomycorrhizae following treatment for *Phytophthora* sp. with metalaxyl.

Water potential to monitor tree water stress was measured quarterly, then semi-annually for a total of 5 years. On each tree, mid-day readings of five sample twigs (5 to 13 cm long) were taken from four cardinal directions in full sun. That night an additional five pre-dawn samples per tree were measured, using either a PMS Scholander Pressure Chamber (PMS Instrument Company, Corvallis, Oregon), or Model 3005 Plant Water Status Console (Soil Moisture Equipment Co., Santa Barbara, California).

Results

The majority of control trees at all sites maintained a stable, healthy condition during the 10-year-study, with the exception of four trees adjacent to installed landscaping that are showing signs of decline from root rot. Despite several periods of drought, all of the unimpacted control trees had vigorous shoot growth and full canopies. A summary of overall tree survival during the course of the study is provided in *table 2*.

Table 2—*Summary of transplanted oak survival.*

Treatment	Dead	Decline	Stable	Good	Improving	Total number of trees
Pruned – 10 years post planting	7	6	8	4	0	25
Pruned – 5 years post planting	7	14	4	0	0	25
Non pruned – 5 years post planting	3	17	10	1	0	31
Non pruned – 5 years post boxing (burned)	7	21	3	0	0	31
Control trees no impact	0	0	4	15	3	22

Change in vigor from before transplanting to present of the non-pruned planted trees was compared to that of the pruned transplanted trees *(fig. 2)*.

Due to the impacts of the wildfire, the non-pruned trees that remained boxed and were burned are not included in the following results.

It is interesting to note that 5 years post pruning, fewer of the pruned trees were in stable or good condition, and more trees had died as compared to the condition of the non-pruned trees. Even after 10 years, the pruned trees have failed to recover their pre-transplant vigor level. It remains to be seen if the non-pruned trees are able to achieve pre-transplant vigor when they reach the 10-year mark. There was no notable difference between the rate of growth or vigor rating between single trunk and multi-trunk trees.

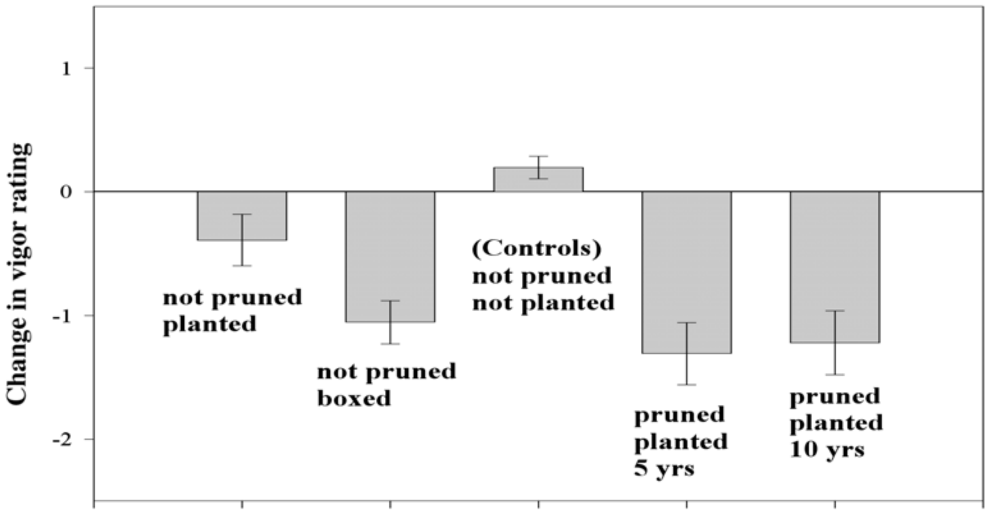

Figure 2—Change in vigor rating of pruned and non-pruned transplanted coast live oaks.

Change in diameter over time reveals additional interesting information. During the first 5 years post planting, the pruned trees did not grow, while the non-pruned trees showed evidence of slow, continuous, growth. However, 5 years post planting, the pruned trees did begin to grow, and by 10 years post planting, they had almost caught up to the rate of growth constantly maintained by the control trees *(fig. 3)*. By contrast, most control trees had visible growth cracks in the trunk bark, indicating continual active radial growth each year. Such cracks on the pruned trees during the first 5 years, if present at all, were smaller and fewer in number. Active radial growth for the non-pruned trees maintained a small, but steady increase.

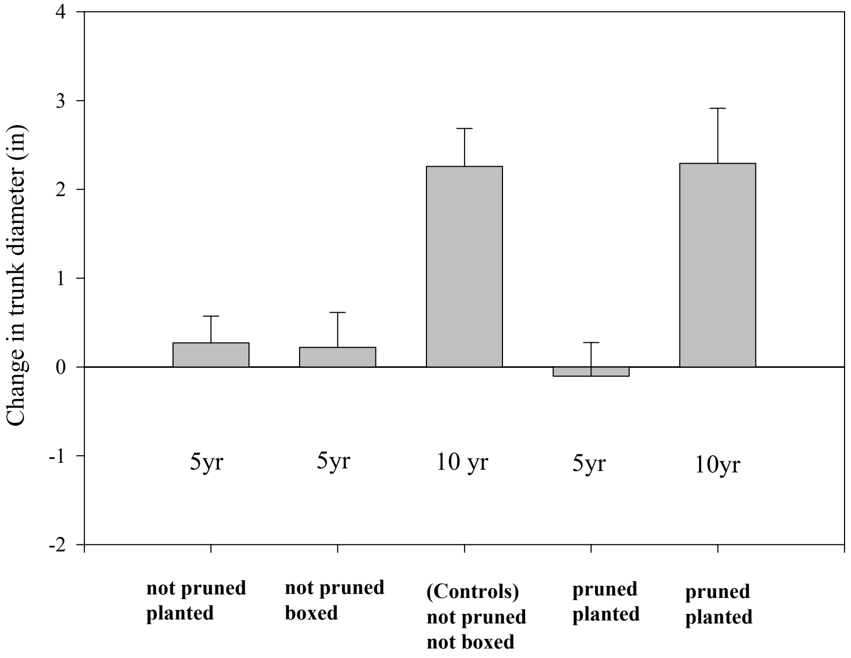

Figure 3—Change in trunk diameter of pruned and non-pruned transplanted coast live oaks.

Control trees maintained a dense canopy and normal branching structure, with few epicormic sprouts. Pruned transplanted trees had little apical growth and their canopies remained characteristically thin, open, and often chlorotic. Trees showing improvement had epicormic growth clustered densely in the center of the tree, thinning out towards the dripline. This pattern was notably different in the non-pruned trees, which maintained a normal terminal growth pattern, with additional epicormic growth appearing after several years. There was no obvious change in the canopy density initially for the non-pruned trees. Canopy loss began after several years, concurrent with overall loss of vigor *(fig. 4)*. Both pruned and non-pruned transplanted trees chronically suffered from twig girdlers (*Agrillus angelicus*) and whitefly (*Aleuroplatus coronatus*) infestations.

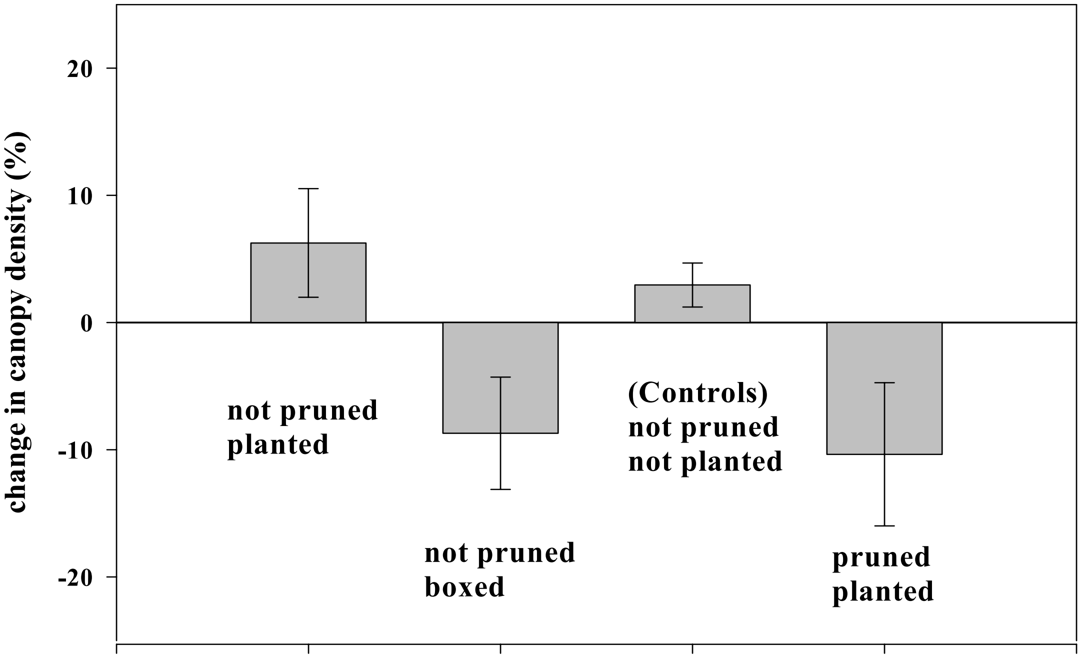

Figure 4—Change in canopy density of pruned and non-pruned transplanted coast live oaks.

There was a marked difference in spring flushing growth patterns between the pruned and the non-pruned trees. Most notable was the difference in distribution of shoots *(table 3)*. While the control and non-pruned trees grew in a normal branch pattern, the pruned trees produced primarily epicormic sprouts from the scaffold branches and trunk, with few shoots emerging from remaining terminal buds.

Table 3—*Comparison of twig growth.*

Treatment (cm)	Avg. no. shoots	Range of shoot length	Range number leaves/shoot
Pruned	2	1-12	5-10
Non-pruned	2	2-18	9-12
Controls	3	5-30	9-18

Analysis of leaf tissues did not indicate any notable differences for the majority of parameters. The optimal range of total nitrogen levels for coast live oaks according to Fruit Growers Laboratory is between 1.15 to 1.21 percent. This is a much narrower range than that for either valley oaks (*Q. lobata*) which extends from 1.2 to 3.5 percent, or for cork oaks (*Q. suber*) which ranges from 1.5 to 2.5 percent (Perry and Hickman 2001). Data from our study found that both the pruned and non-pruned coast live oak transplants had broader ranges from 1.4 to 2.6 percent, while the control trees in the study were between 1.4 to 2.1 percent. However, no statistically significant differences in total nitrogen levels were found according to a paired t-test ($p<0.05$).

There did appear to be a more significant difference between calcium levels. Control trees had levels averaging 1.06 percent. The pruned trees averaged 0.86 percent and the non-pruned trees averaged 1.03 percent *(fig. 5)*.

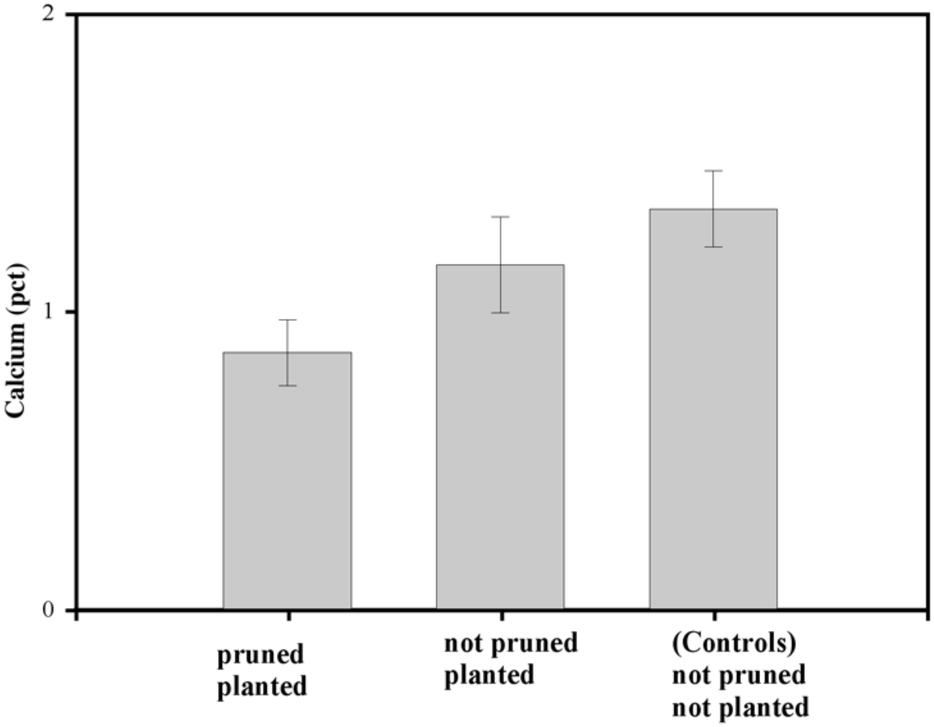

Figure 5—Comparison of average percent calcium levels in leaf tissues of pruned and non-pruned transplanted coast live oaks.

Among the non-pruned transplanted trees at Site 4, root density was not apparently related to tree vigor. As a result of mycorrhizal inoculations and mulching, both the planted and boxed transplants had greater fine root (<5mm) density than the control trees, which received no inoculations or additional mulching. There was no significant difference between root density of planted vs. boxed non-pruned trees. Interestingly, the rate of infection by root pathogens (*Phytophthora* sp.) decreased following the mycorrhizal inoculations, as did the percentage of beneficial fungi and protozoans. It appears that the inoculations and additional mulching were successful in improving the soil foodweb conditions. No comparable data was available for the pruned trees.

A plot of the water potentials of transplanted trees and final vigor rating suggests that there is no statistical relationship. However, a few trends were apparent. Variability in readings between trees was greater in both the pruned and the non-pruned transplants, with control trees remaining more consistent at any given time. No statistical comparisons were made for individual data from the same dates. Control trees (receiving no irrigation) did show lower summer/fall water potential (July and October), but they rarely dropped below a pre-dawn potential of –2.5 MPa. By contrast, declining transplanted trees routinely exceeded that limit. In nearly dead trees, pre-dawn water potentials exceeded those at mid-day.

Discussion

We observed steady tree decline resulting from transplantation, although the non-pruned trees initially maintained better vigor, canopy density, and growth than the pruned trees. Impacts reported from removing the majority of the root system and canopy were manifested in the transplants by disrupted water relations (Tyree and others 1994), loss of internal hormone relationships (Coder 1994), changed carbohydrate balance (Holinger 1992), and stress-induced pest/disease problems (Hagen 1989). Irrigation and drainage problems probably added to the stress of all the transplants, but were not significantly different between the non-pruned and the pruned trees.

Regeneration of lost root and canopy tissue is related to tree size and maintenance conditions (Watson 1994). For each 2.54 cm of trunk diameter, root replacement took approximately 1 year in the Midwest (Watson 1985). The pruned trees struggled to regain lost resources, and are just beginning to stabilize 10 years post transplanting, finally exhibiting symptoms of root recovery.

The data indicates that the non-pruned trees are less stressed initially, providing greater opportunity for eventual establishment. Heavily pruned trees are handicapped by disruption of the xylem–phloem system for distributing water, nutrients and photosynthate throughout the trees. For example, severe pruning can effectively “starve” the roots if the foliage on the lower and inner branches is removed, preventing materials from reaching the roots. This leads to less root exudate leaching into the soil and reduces nourishment for symbiotic soil organisms in the rhizosphere. Water is less effectively recycled throughout the tree and the delicate feedback loop between the roots and the canopy is further stressed (Ringgenberg 2001).

Calcium concentrations in leaf tissue are also indicative of the complex impacts to metabolic processes resulting from transplanting. Leaf tissue levels of calcium in the control trees were significantly better than those found in the transplants, although the non-pruned trees were in better condition than the pruned trees. Calcium is essential to both shoot and root growth, and low levels are observed when new growth is stunted (Harris 1992). Although sufficient calcium is generally present in the soil, its uptake is regulated by complex interactions that are clearly disrupted by severe root loss and canopy reduction. The role of the soil foodweb in facilitating nutrient uptake is also critical, and transplanted trees with disturbed and deficient microbial communities are not able to support the nutrient cycling necessary to optimally invigorate the tree (Ingham 2001).

Preliminary results of tests to identify preferred locations of carbohydrate storage in pollarded London Plane trees found that while the tree remained pollarded, carbohydrate storage remained near the heading cuts, with little found at other locations in the tree. Trees that are not pruned store carbohydrates primarily in the woody roots, root crown, branches, and at the base of the trunk (Svihra, personal communication). If this is true of oak species as well, it would further explain why the trees take so long to recover from the loss of 90 percent of their root system, including the majority of woody roots containing stored carbohydrates. Oaks are known for their ability to store extensive energy reserves, and loss due to root pruning clearly has a significant impact on the tree (Rundel 1980). It is clear that 10 years is the minimal monitoring period needed in order to begin to understand the full impacts of transplanting on the physiology of coast live oaks.

It appears that canopy retention and mycorrhizal inoculation make a positive difference on transplanting success. Even with additional improvements, such as boxing one side at a time over 12 months (Himelick 1991), it may be that the highest attainable level of care would not be sufficient to overcome the trauma of transplantation for the majority of mature coast live oak trees. While both the pruned and non-pruned transplanted trees remained alive, they were no longer self-sustaining, but rather high-care exotics that require intensive, long-term maintenance.

The cost of boxing each tree in this study varied from $1,000 to over $100,000 dollars, totaling almost a million dollars for all 130 trees. Given the high cost of moving, maintenance and monitoring (approximately $80,000 per year for 10 years, and counting), it appears that a low establishment rate fails to justify the expense.

Conclusions

Initial recovery of coast live oaks from transplantation appears to be enhanced by retaining the natural canopy. After 5 years, only 14 percent of transplanted pruned trees in this study showed signs of establishment, compared to 35 percent of the planted, non-pruned trees. Additionally, 28 percent of the pruned trees were dead, compared with 10 percent of the non-pruned trees. All of the transplanted trees continued to require extensive care and maintenance. Even with the eventual improvement shown by the pruned trees 10 years after transplanting, they have still failed to recover their original level of vigor. While retaining the natural tree canopy appears to reduce initial loss of vigor following transplanting, it remains to be seen if the long-term survival of the non-pruned trees is significantly better than that of the pruned trees.

It is also important to note that the initial mortality of trees immediately following boxing is frequently ignored when tree-moving companies quote statistics about tree survival. Of the 130 oaks boxed for this study, 32 percent died (42 trees: 5 pruned, 37 non-pruned) immediately following boxing, and were not included in the study results. The high initial mortality of the non-pruned trees was a result of a financial crisis, which left the developer unable to maintain the trees once they were boxed. The financial uncertainty involved in the development process needs to be factored in, since loss of funding is a common problem, leaving many transplanted trees without care. Posting of bonds to cover the monitoring and maintenance of transplanted trees should be required.

If the goal of mitigation is to replace lost natural resources, then the cost-effectiveness of transplanting oaks needs to be carefully examined. The impetus for moving large oaks comes from the increased property value associated with mature landscapes and the desire of developers to appear to be environmentally conscious. However, isolated oak trees distributed throughout a suburban development do not have the same ecological value as a grove of trees with their undisturbed habitat. A more pragmatic approach to mitigation would be to use transplantation monies to purchase and dedicate as open space existing oak woodlands. While there may be a few instances where moving an individual tree is warranted, all involved should be aware of the high long-term costs involved in supporting a severely damaged tree.

Another consideration should be the placement of the tree in the landscape. By definition, transplanted oaks are considered to have high hazard potential associated with severe root loss. Placement of trees in open space areas away from possible "targets" (such as picnic benches, walkways, buildings and roads) should be required. Oaks are also highly susceptible to infection with *Phytophthora cinnamomi*, a common landscape pathogen. Summer irrigation necessary to support transplanted trees creates conditions that foster root diseases. All of the transplanted trees were treated with an appropriate fungicide to inhibit *P. cinnamomi*.

The results of this study indicate that while transplanting success is enhanced initially by retaining the natural canopy of coast live oak trees, the physiological response of the trees to the trauma is still extreme, recovery is limited, and the costs are high. Transplanting coast live oaks does not appear to be an effective mitigation practice to replace lost oak woodlands.

Acknowledgments

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Supersonic Air Jets Preserve Tree Roots in Underground Pipeline Installation[1]

Rob Gross[2] and Michelle Julene[3]

Abstract

Tree roots are often damaged during construction projects, particularly during trenching operations for pipeline installation. Although mechanical soil excavation using heavy equipment, such as an excavator or backhoe is considered the fastest the most economical method, it damages and destroys tree roots and can lead to unintentional tree loss, poor public relations, fines, and litigation. In sensitive areas around tree roots, soil excavation can be completed by hand although this is very slow and expensive. Alternate soil excavation methodologies are available, including a special technique that uses supersonic air streams to explode soil around non-porous items such as pipes, fiber optic cables, sewer and phone lines, and tree roots. This paper discusses the use of this technique for "high value" coast live oak trees (*Quercus agrifolia*) in urbanized areas. A case study is presented that discusses an appropriate application of the pneumatic soil excavation method. The pneumatic method is a valuable technique for root zone soil excavation. It preserves tree roots during construction to allow retention of the structural integrity of the root system and provides an opportunity to accurately understand actual root, soil, and tree conditions. This improves discussions with an affected tree owner, or other interested party, regarding future management options of the tree.

Introduction

Utilities of many types are routinely installed, repaired, and replaced underground. During soil excavation, tree and other plant roots are destroyed when conventional soil excavation methods are used. Conventional soil excavation methods utilize heavy machinery, such as excavators and backhoes that rip away plant roots as the construction trench is created. In terms of construction cost, conventional soil excavation is the least expensive method because it does not require special construction tools, equipment, training, or extra time. In terms of preserving trees, conventional soil excavation could be the most costly method because the ripping away of tree roots severely compromises tree heath, often resulting in tree fatality.

Alternative soil excavation methods exist that preserve tree roots. These methods include manual, hydraulic, and pnuematic soil excavation methods. The manual soil excavation method utilizes hand tools, such as shovels, to remove soil from the root zone. The benefits of the manual soil excavation method include the use of inexpensive, common hand tools and minimal training. The drawbacks of this method include the length of time required to fully excavate the root zone, which could translate to a substantial increase in overall project costs. An additional

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drawback to the manual soil excavation method is that, while large roots are preserved, they are scraped and smaller diameter roots are often broken. The manual soil excavation method is more appropriate to excavate small areas of soil.

In recent years, the hydraulic soil excavation technique has been refined (Gross 1995). The hydraulic soil excavation method utilizes water to remove soil from the root surface. The soil excavate is converted into a slurry. One application for using hydraulic excavation on oak roots is reported by Lindsey and others (Lindsey 1995). The primary benefit of the hydraulic soil excavation method is that the method is the most powerful, and therefore the fastest, of the alternative soil excavation methods. Hydraulic soil excavation can result in minimal observable impacts on living roots, and once excavated, the roots can be inspected if desired. There are several drawbacks to this soil excavation method, such as available water supply, specialized equipment, training, and the slurry itself. Specialty equipment, including hose and nozzles to implement the excavation process as well as vacuum pumps to clean-up the slurry, can be expensive. Training is required to operate the equipment and to understand the appropriate water pressure application rate to specific ground and root conditions. The slurry itself presents several concerns. The excavated soil, when mixed together with the water in the excavation process, can increase the waste volume up to ten fold. This slurry cannot be used as trench backfill and therefore must be removed from the site. Slurry removal requires additional equipment and can result in additional disposal costs if landfill disposal is necessary. Because the slurry cannot be used as trench backfill, new soil must be imported, often at additional cost. The slurry also creates a potential slip and fall hazard at the excavation site and the moistened soils along the trench walls are more likely to cave in than are dry soils. The hydraulic soil excavation method is recommended for high volume excavations, in which trench depth and clean up are not issues.

The pneumatic soil excavation method forces rapidly moving air into the soil pores until they fail in a series of small explosions away from non-porous objects, such as underground utilities and plant roots. The excavated soil is transformed into crumbs that are relocated. The primary benefit of the pneumatic soil excavation method is that it protects tree roots, including small diameter and fine roots. Additional benefits of the pnuematic soil excavation method include unlimited air supply, relatively minimal clean-up, and re-usability of the excavate. Another benefit of the pneumatic soil excavation method is that it can be used along with conventional machinery after the root zone is excavated of soil. First, the soil among the roots is excavated using the pneumatic method. Then, a conventional excavator or backhoe can be used below the root level to increase trench depth at an increased production rate, while avoiding root damage. Combined, this hybrid process is particularly efficient. This allows trench construction, particularly for deep trenches, to proceed at a more efficient rate of speed. Drawbacks of the pnuematic soil excavation method include the need for special equipment and training. In addition to the specialized nature of the tools, they can overheat while in use and high ambient temperatures reduce excavation efficiency. The pneumatic soil excavation method is recommended for high value trees, in settings where a trench must be dug below three feet deep, and when considerations such as clean-up, safety, and construction production time exist.

The subject case study involved a construction trench for an underground utility installation in a residential area. The community of Mirabel Heights in Sonoma County, California originally was developed as a summertime vacation community in the 1940s. By the 1980s, it had converted to fully residential and over 70 percent of the septic systems were failing. Small septic tanks were placed on small, hilly lots. Streets were paved in the 1960s and a water distribution system was installed in subsequent years. The sewer installation project cost approximately $4 million for approximately 200 homes. Project planning, environmental compliance, and approval took more than 10 years to complete. This project included installation of a sewer transmission pipeline in a residential area. The trenches would be two feet wide and would exceed a ten-foot depth in some places. Due to extremely narrow roads, the construction trench would begin within three feet of the trunk of the subject tree (Sonoma County Water Agency 1999).

In this case study, the subject coast live oak tree (*Quercus agrifolia*) was considered to be of high value by the property owner. The property owner stressed that the tree increased his property value, adding up to $50,000 to his property value, although a valuation report was not produced. The property owner demonstrated a considerable attachment to the tree, and admitted to spending large sums of money to an Arborist throughout the years for tree care. The property owner requested that the pipeline alignment be relocated to minimize or avoid impacts to the tree. The property owner suggested that the pipeline be moved onto private property across the street from the tree, and if that were not possible, then to move the pipeline an additional two to three feet from the design location.

The property owner had contacted his Arborist and Attorney in case the tree fell or died due to the construction, and communicated these actions verbally and in writing to the Agency. The property owner also threatened to litigate if the tree was damaged or lost due to the construction project. The Agency's Environmental Specialist and Consulting Arborist were brought in to document the overall condition of the tree, assess potential impacts of the Project on the tree, and develop recommendations to reduce potential impacts. The property owner agreed to this consultation. The initial assessment of the tree revealed that the tree was large sized, in poor health, was structurally compromised, had received poor quality arboricultural care, and was severely impacted by landscape surroundings.

The tree's canopy extended across the street and onto private property across the street. Lesions were observed on the low trunk bark near the soil line, suggesting that a root rot was involved. Armillaria root disease was observed at the root collar and into the sapwood. This was determined visually after removing portions of the bark. The trunk base was hollow at ground level and also at approximately twelve feet from the base. A cement-filled cavity was located at six feet from the base. The tree had been topped repeatedly. There were no lower limbs. Two large limbs were cabled together using ½-inch diameter wire rope, which was wrapped around these limbs and girdled them. Foliage was thin, with leaves on only 40 percent of the potential canopy. Poor arboricultural procedures had resulted in an uncommonly weak structure and contorted tree shape. The presence of Armillaria root disease also indicated poor tree health, as this species of oak is usually immune to highly resistant to this fungus (Raabe 1979).

Site conditions surrounding the tree not only contributed to the tree's overall condition, but also limited placement of the construction trench. The tree was located adjacent to and above the property owner's driveway on a small lot. The paved public road surface began within one foot of the base of the tree trunk. Existing utilities were located in the paved public road. Surrounding soil surface was compacted due to previous construction and heavy, on-going use surrounding the tree including the property owner's garage and driveway. Even though the tree was in poor health and unfavorable site conditions were present, the pneumatic soil excavation method was recommended to improve public relations and avoid potential litigation. In this case study, it was necessary to conduct careful soil excavation and trench construction to demonstrate significant effort to the property owner towards minimization of tree impacts. The conventional method would have destroyed tree roots, possibly resulting in tree fatality and litigation. The manual method would have been too slow and the hydraulic method would not have been appropriate for this application, due to the depth of the construction trench.

Methods

In the subject case study, the pneumatic soil excavation method was conducted using an Air Knife, model XL 150/90, to explode soil around tree roots. A rushing air stream, accelerated to twice the speed of sound (Mach 2), was focused in the root zone and filled soil pores. The rapidly building air pressure created a series of small explosions. As the soil exploded, it was forced away from the tree roots and was transformed into small crumbs. The pneumatic soil excavation method was conducted only within the top three feet of soil because ninety percent of most tree roots were located in this space. After the soil was excavated, the preserved root system created a "tree root bridge" free of soil, beneath which conventional mechanical soil excavation was employed to achieve the required trench depth. Skilled combination of pnuematic soil excavation in tandem with the excavator or backhoe beneath the tree root bridge maintained construction production and root integrity.

Results

With the use of the "root friendly," pneumatic soil excavation technique, soil was successfully removed from the tree root area and tree conditions were observed. This soil excavation technique allowed retention of the tree root bridge, a depth of approximately three feet below the soil surface. Beneath the tree root bridge conventional trench excavation utilizing a backhoe was completed to achieve a trench depth of approximately ten feet. In addition to the successful excavation of soil in the root area and completion of trench excavation, pnuematic soil excavation permitted the discovery of poor tree health and poor structural integrity. Because the roots were not damaged during soil excavation, the property owner was able to visually inspect the tree roots and the Agency's Environmental Specialist and Consulting Arborist were able to discuss the tree's condition and alternatives with the property owner. Soil removal within the root zone led to the discovery of the following:

1. Prior installation of an underground water pipe resulted in cutting the tree's roots approximately 14 feet north of the tree trunk and road construction, which occurred within one foot of the tree trunk, also severed tree roots.
2. The roots in the excavated trench were three to four inches diameter and the soil surrounding them was compacted. No white roots were observed. This suggested anaerobic conditions or a rootlet disease. Phytophthora root rot is one disease that commonly kills rootlets. Rootlet loss weakens trees and would partially explain why this tree contracted Armillaria root disease.

3. The excavated trench exhibited no healthy roots. Numerous voids observed in the trench faces indicated where roots had previously been, but had long since decayed. Some roots suffered from advanced decay indicated by a watery soft consistency. Most of these roots exhibited dead bark, white fungal mycelium at the cambium, and white rotted wood, which indicated a pathogenic colonization (Baumgartener and Rizzo 2001b). The roots and part of the lower trunk were being attacked by Armillaria root disease, which is widely distributed in most regions of California dominated by development, such as the San Francisco Bay Area (Baumgartner and Rizzo 2001a).
4. No healthy roots were cut in the pneumatic soil excavation process.
5. The opportunity to discover actual soil and root conditions allowed the tree owner to see and understand that the tree was compromised prior to construction.

Discussion

In this case study, the Agency's Environmental Specialist and Consulting Arborist were presented with a difficult challenge. A necessary underground utility was being installed in a residential neighborhood with very narrow streets. A property owner, who had an oak tree on his property, threatened litigation if the construction project adversely impacted his tree. Visual inspection of the tree indicated that the specimen suffered from numerous and severe health and structural problems as well as a compromised growing environment. Nonetheless, the Agency's Environmental Specialist and Consulting Arborist were challenged to recommend and perform a soil excavation method that would minimize potential tree impacts without resulting in significant construction production delays.

Three primary issues were considered in deciding which soil excavation method would be most appropriate. These issues included tree preservation, minimal delay in construction, and relative overall cost. The conventional soil excavation method was eliminated as an option because the tree roots would have been destroyed thereby resulting in substantial tree impacts. The cost of the potential litigation and poor public relations, as well as future potential tree removal costs, would have significantly increased the overall cost of the project. The manual soil excavation method was eliminated as an option because it would have slowed construction production to an unacceptable level, which also would have significantly increased the overall cost of the project.

The hydraulic and pneumatic soil excavation methods were considered as possibly appropriate. Rizzo and Gross (2000) compare hydraulic and pneumatic techniques. Harris and others (1999) discuss hydraulic and pneumatic for locating roots. Both methods would have preserved the tree roots, would have resulted in minimal delay in construction production, and would have similar relative overall cost. The hydraulic soil excavation method was determined to be inappropriate in this case due to the necessary trench depth. The moistened soil would have rendered the construction trench more subject to failure at the necessary depth. The pnuematic soil excavation method was determined to be the most appropriate method within the root zone of the subject case study.

The pnuematic soil excavation in combination with conventional methods using a backhoe was particularly effective and met the objectives of the task. The tree roots were preserved thereby minimizing tree impacts, construction production was maintained, and the additional cost of excavating the soil carefully was minor when compared to the cost of potential litigation. The pnuematic soil excavation technique is recommended for "high value" trees, whatever the criteria. In our example, the Mirabel Heights tree was considered to be a high value tree by the property owner even though the specimen was in poor health.

In the subject case study, the pnuematic soil excavation technique allowed us to observe Armillaria root disease and other root system limitations. Because the pnuematic soil excavation preserved the tree roots, including those affected by Armillaria root disease, we were able to discuss the condition of the tree with the property owner, improving communication regarding future management of the tree. Pnuematic soil excavation is a valuable technique for root zone soil excavation, as it preserves tree roots during construction to allow retention of the structural integrity of the root system, and provides an opportunity to accurately understand actual tree conditions, thereby improving communication.

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The Influence of Treeshelters and Irrigation on Shoot and Root Growth of Three California Oak Species[1]

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Abstract

Treeshelters are individual seedling protectors that can accelerate height growth of native California oaks. There is concern, however, that this growth may occur at the expense of the roots, resulting in poor long-term field performance. This study could detect no differences between protected and unprotected seedlings in shoot weight, root weight or shoot/root ratios after 4½ years, suggesting that shelters do not adversely affect balances between seedling shoots and roots. Shelters did, however, stimulate height growth and reduce initial stem diameter growth, resulting in tall narrow plants that might not be able to stand upright without staking if shelters are removed too early. This study also evaluated the effects of irrigation levels on growth of three oak species—blue oak (*Quercus douglasii*), valley oak (*Q. lobata*) and coast live oak (*Q. agrifolia*). There were no significant differences among irrigation levels, suggesting that, in environments similar to the study site or in areas with fertile deep soils, supplemental irrigation after initial establishment is not necessary. Finally, the extremely rapid growth of both the valley oak and coast live oak in this study indicates that these species show promise for planting in urban landscapes.

Introduction

During the past two decades there has been increasing public concern about conservation and management of native oaks in California. Poor natural regeneration of several oak species has been repeatedly identified as a problem. Until recently, however, relatively little was known or understood about the biology of California oaks in general or regeneration processes in particular. Concerns about regeneration have led to a number of studies aimed at developing successful procedures for artificial regeneration of native oaks (Adams and others 1991, McCreary 1989). However, most of this research has been conducted on relatively harsh rangeland sites, such as Sierra Foothill and Hopland Research and Extension Centers (SFREC

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and HREC). Consequently, there is little information about the best procedures for establishing oaks in landscape settings where opportunities for more intensive management are possible.

One device that has shown particular promise for establishing oaks on rangelands is the treeshelter (Costello and others 1996, McCreary and Tecklin 1997, Tecklin and others 1997). These are double walled translucent tubes that protect seedlings from a number of damaging animals. They also stimulate aboveground growth by changing the environment seedlings are exposed to, including higher levels of CO_2, higher temperatures, and increased humidity (Potter 1991). However, some feel these devices may produce “unnatural” plants that are ill adapted to survive after the shelters are removed. This is because plants in treeshelters tend to grow tall and thin and may be unable to stand upright when shelters are removed. It has also been suggested that treeshelters may cause a preferential allocation of photosynthate to shoots. As a result of such carbon allocation, plants may be out of balance and not develop sufficiently large root systems to support their tops. It is not known, however, if such imbalances occur or how long they might last.

Finally, most research on oak regeneration in California has been with blue oak. This species has been identified as having poor natural regeneration and since it is widely distributed, there has been great interest in determining why regeneration is inadequate and how to overcome this problem. However, in urban or landscape settings, other native oak species may be preferable for planting because they have the potential to establish more quickly and grow faster.

This research project was designed to evaluate the performance of three species of native oaks planted in a horticultural setting, provided different levels of irrigation, and either protected with treeshelters or left unprotected. Annual height and diameter growth were monitored for 4½ years and total root weight, total shoot weight and shoot/root ratio were measured at the end of the study.

Methods

This study was conducted at Bay Area Research and Extension Center (BAREC) in Santa Clara. This Center offers a much different environment than SFREC or HREC since it has deep, uniform, agricultural soils, providing an opportunity for high levels of management. The field site was tilled and all weeds removed prior to planting. The soil, which is over a meter deep, is classified as a Campbell silty-clay loam.

In January 1997, pregerminated acorns of blue oak (*Quercus douglasii*), valley oak (*Q. lobata*) and coast live oak (*Q. agrifolia*) were planted in a field plot consisting of 4 blocks, each with 72 planting locations. Each block contained three irrigation treatment groups (24 seedlings). Irrigation treatments were 0.50 ETo (reference evapotranspiration), 0.25 ETo, and 0 ETo (control). Reference evapotranspiration was determined by a CIMIS (California Irrigation Management Information System) station located at BAREC. During the middle of summer ETo averages about 4 cm per week at BAREC.

All seedlings were irrigated during the first growing season with sufficient irrigation to ensure establishment, but no irrigation was provided to controls thereafter. The pressure compensating drip irrigation system provided water to an area approximately 20 cm by 20 cm around each planting location once a week through 3.6 liters-per-hour drip emitters. Irrigation continued until the fall rainy period. Irrigation was initiated in subsequent years in the summer and continued until there was 5 cm of rain in the fall. For the 0.25 ETo treatment, 3.6 liters of water per week were provided. For the 0.50 ETo treatment, seedlings were given twice this amount.

Within each of the 24-seedling irrigation plots, acorns were spaced 1.2-m apart. Each plot was separated from other plots by 2.4 m to ensure that irrigation treatments did not influence seedlings in adjacent plots, and a buffer row of seedlings was planted around the entire perimeter of the study area. Within each irrigation plot were three pairs of four-seedling rows. Each pair was randomly assigned to be planted with acorns from one of the three species. In addition, one of these rows from each pair was randomly assigned to have a 1.2-m treeshelter placed over emerging seedlings, while seedlings in the other row were left unprotected. All acorns were planted within a 2-day period.

Height and Diameter Measurements

Seedlings began to emerge in March 1997. At the end of the year, the height of each surviving seedling was measured and recorded. Height was the distance from the base of the seedling to the end of the longest shoot held straight. At the end of 1998 and 1999, the height, as well as the diameter, of each seedling was measured. Diameter measurements were taken at the base of each seedling, approximately 2 cm above the ground.

Final field assessments were made in mid-2001. Height was measured in May. In contrast to previous measurements where the longest terminals were measured, by mid-2001, many of the coast live oak trees were so tall that it was not possible to measure them this way. Therefore heights for this species were recorded as the distance from the base of the tree to the tallest portion of the plant. Diameters for all species were measured as before.

Root Excavation and Measurements

An objective of this study was to determine how shelters and irrigation affect root development and, in particular, whether treeshelters increase shoot growth at the expense of root growth. To determine this, we excavated, weighed, and measured root systems. However, since excavations are difficult, expensive, and time consuming, we excavated only a sub-sample of saplings in the study. We excavated all surviving saplings in one of the four blocks. Unfortunately, we were also constrained by the fact that one of the species, coast live oak, is susceptible to a new and potentially devastating disease called Sudden Oak Death, caused by the pathogen *Phytophthora ramorum*. Since BAREC is located in one of the infected counties, there was a quarantine on movement of coast live oak plant parts outside the county. Since our root evaluation procedures required us to take all of the harvested trees back to Sierra Foothill Research and Extension Center in Yuba County to dissect, measure and weigh, we elected to concentrate our root excavation and assessment on blue oak and valley oak and not evaluate the roots of coast live oak.

A backhoe was used excavate a 1.2-m deep hole on either side of each sapling, approximately 1.2 to 1.8-m from the trunk. The narrow bucket of the backhoe was used to carefully reach into the root zone and loosen the soil. The trunk of the sapling was then secured to a chain, which was hooked to the bucket of the backhoe. The bucket was rocked back and forth to loosen the soil in the rooting zone, and finally the chain was raised slowly, lifting the sapling and pulling it out of the ground. This worked quite well and seemed to provide a good, though not complete, recovery of roots. We estimated that approximately 10 percent of the roots was left behind, based on where and how thick some of the roots were that broke off. However it was not possible to accurately estimate how many of the finer roots were not recovered. In several cases, more roots broke and remained in the soil than we felt were acceptable; we excluded these from our sample.

Excavated trees were brought to SFREC, air dried in a warehouse for approximately two weeks, and then cut at root crown (the ground line), and separated into shoots and roots. These were placed in a drying oven for 5 days at 70°C. Prior to drying, all woody material was cut up into 10 to 15-cm segments. Dry weights for shoots and roots for each tree were recorded and shoot/root ratios were calculated.

Prior to drying and weighing, the diameters of the roots at various depths were also measured, and the roots were separated into various fractions (i.e. upper tap root, lower tap root, lateral roots) for weighing. In this paper we only report on total shoot and root weights and shoot/root ratios. A subsequent paper will describe root size and distribution in greater detail.

Statistical Analysis

Field data including survival, height and diameter were analyzed for a doubly nested, randomized block design, with irrigation levels as main plots, species as sub-plots, and protection treatments as sub-sub-plots. The data for these analyses were averages of the four-seedling rows within each block, irrigation treatment, species and type of protection (treeshelter or control).

We did not have enough observations to statistically analyze the shoot and root weight data as above, since only 31 sample trees were recovered with useable, excavated roots. We therefore analyzed shoot weights, root weights and shoot/root ratios for treatment effects using one-way analyses of variance.

Results

Survival

There were no significant differences in survival among any treatments during any year of the study. Average survival at the end of the first year (1997) was 82 percent, but remained fairly constant thereafter, falling to 79 percent by the last evaluation in 2001 *(table 1)*. One factor that appeared to contribute to initial mortality was that in some treeshelters rainwater did not drain adequately and some tubes filled several inches with water. When we observed this, we made holes in the bottoms of the shelters to drain the water, but there was probably some acorn mortality due to poor drainage.

Table 1—*Survival (pct) of acorn plantings for different species and treatments between 1997 and 2001.*[1]

	Survival '97	**Survival '98**	**Survival '99**	**Survival '01**
Species				
Blue oak	75	75	75	74
Valley oak	82	81	81	80
Coast live oak	88	84	88	83
Protection				
Treeshelters	81	80	80	80
Control	82	81	81	81
Irrigation				
No water	78	77	78	76
0.25 evapotranspiration	85	84	85	83
0.50 evapotranspiration	81	79	80	78

[1] There were no significant differences in survival in any year among species, protection treatments or irrigation treatments. Some survival percentages increased between 1998 and 1999 because of resprouting from apparently dead tops.

Height

Significant differences in height were found among species in each year of the study. During the first and second years (1997 and 1998), valley oaks and coast live oaks were significantly taller than blue oaks, but not different from each other *(table 2)*. By the last two years, there were significant differences between all three species, with coast live oaks the tallest, valley oaks next, and blue oaks the shortest.

Trees in treeshelters were significantly taller than trees without shelters in every year of the study. However, on a percentage basis, these differences tended to decline over time. There were no significant differences in height among irrigation treatments during any year of the study.

Table 2—*Average height (cm) for different species and treatments between 1997 and 2001.*[1]

	Height '97	**Height '98**	**Height '99**	**Height '01**
Species				
Blue oak	41 a	99 a	171 a	204 a
Valley oak	91 b	156 b	213 b	258 b
Coast live oak	75 b	159b	256 c	329 c
Protection				
Treeshelters	89 a	167 a	240 a	288 a
Control	50 b	108 b	187 b	240 b
Irrigation				
No water	63	127	200	244
0.25 evapotranspiration	67	141	211	269
0.50 evapotranspiration	77	145	229	279

[1] Within treatments (irrigation and protection) and years, heights with different letters are significantly different by a Fisher's Protected Least Significant Difference (LSD) Test. There were no significant differences in any year among irrigation treatments.

Diameter

Differences in diameter among species followed a pattern similar to that for height. For every annual evaluation, there were significant differences among species with coast live oaks having the largest diameters, followed by valley oaks and blue oaks *(table 3)*.

Table 3—*Average diameter (mm) for different species and treatments between 1997 and 2001.*[1]

	Diameter '98	**Diameter '99**	**Diameter '01**
Species			
Blue oak	11.5 a	19.9 a	34.1 a
Valley oak	16.1 b	25.1 b	42.0 b
Coast live oak	22.7 c	42.3 c	77.1 c
Protection			
Treeshelters	14.9 a	26.8 a	46.9 a
Control	18.6 b	31.4 b	55.2 b
Irrigation			
No water	15.5	27.0	45.1
0.25 evapotranspiration	16.5	28.9	52.1
0.50 evapotranspiration	18.2	31.4	54.6

[1] Within treatments (irrigation and protection) and years, diameters with different letters are significantly different by a Fisher's Protected Least Significant Difference (LSD) Test. There were no significant differences in any year among irrigation treatments.

Each year there were also significant differences between trees protected with treeshelters and those unprotected. However, in contrast to height, treeshelters produced plants with smaller stem diameters. As with all other variables, there were no significant differences in stem diameter among irrigation treatments.

Shoot and Root Weights

Valley oaks grew considerably larger than the blue oaks, and consequently, had significantly greater shoot and root dry weights. However there were no significant differences in shoot/root ratio between species. In addition, no significant differences in shoot dry weight, root dry weight or shoot/root ratio between irrigation or protection treatments were found *(table 4)*.

Interactions

There were several significant interactions in the analyses of height and diameter. In most cases this was because coast live oak had less of an increase in height for trees in treeshelters than the other two species. This species also had a greater decrease in diameter for trees in treeshelters. The only other significant interaction was between irrigation and species for the final assessment of diameter: the rankings of species were the same for each irrigation treatment, but the relative values were different.

Table 4—*Average shoot weights, root weights and shoot/root ratios for saplings harvested in July, 2001.*[1]

	Shoot wt. (gm)	Root wt. (gm)	Shoot/root ratio
Species			
Blue oak	945 a	742 a	1.32
Valley oak	2,100 b	1,393 b	1.55
Protection			
Treeshelters	1,451	987	1.52
Control	1,577	1,154	1.31
Irrigation			
No water	1,901	1,316	1.27
0.25 Evapotranspiration	1,445	953	1.60
0.50 Evapotranspiration	1,160	947	1.30

[1] There were significant differences in shoot weight and root weight between valley oak and blue oak saplings by a Fisher's Protected Least Significant Difference (LSD) Test. There were no other significant differences.

Discussion

In several studies treeshelters have been found to increase the growth of native California oaks (Costello and others 1991, McCreary and Tecklin 1997, Tecklin and others 1997). In two trials with coast live oak and valley oak, however, Burger and others (1996 and 1997) reported that while plants in treeshelters initially grew taller, by the second year there were no significant differences in height compared with unsheltered plants. Burger and others (1992) also reported that for oaks grown in containers for 2 years in a nursery, treeshelters reduced root dry mass, root/shoot ratio, total root length, and total root weight for valley oaks, as well as above-ground biomass for valley oak and coast live oak. However these studies were of relatively short duration and ratios might have changed if the plants were observed longer. Ponder (1996), for instance, found that tree-sheltered northern red oak (*Quercus rubra*) seedlings harvested 3 years after outplanting in forest openings had both higher stem and root weights than seedlings not protected with treeshelters.

In this study, treeshelters promoted height growth for all species, but produced smaller stem diameters. As a result, shoot dry weight was not significantly different between protected and unprotected plants. Total root weights were similar and, as a consequence, there were no significant differences in shoot/root ratios. Treeshelters therefore did not cause a preferential distribution of photosynthate to top growth. On the other hand, it is clear that treeshelters did alter shoot morphology by creating trees that were taller, but with thinner trunks. Results indicated, however, that this characteristic diminished over time. This is very consistent with a study conducted recently at Sierra Foothill Research and Extension Center with several sizes of treeshelters (McCreary and Tecklin 2001). The key benefits of shelters, therefore, are protecting plants from damaging animals and promoting rapid initial height growth. These are important factors in a number of landscape situations, as long as the shelters are left in place long enough for the plants to develop sufficient girth to become self-supporting.

There were no significant differences for any variable among irrigation treatments. We believe that one of the main reasons we did not observe differences was the fact that this study overlapped an El Niño period in California when annual precipitation was well above normal. As a result, plants in all treatments probably had adequate natural water for near maximum growth.

Rapid growth of both valley oak and coast live oak was notable. Even though native California oaks have a reputation of growing slowly, coast live oak averaged well over 3.3 m (10 feet tall!) after 4½ growing seasons, and valley oaks averaged 2.6 m, with some plants of both species nearly double these averages. Even after the first growing season, many seedlings from these two species (especially those in treeshelters) were over 2-m tall after being planted as acorns. Clearly, both of these species show great promise as landscape plants due to their good survival and rapid early growth.

Conclusions

Results indicate that valley oak and coast live oak can grow rapidly when planted from acorns in good quality soils. Protecting these species, as well as blue oak, with treeshelters promotes rapid initial height growth, but reduces stem diameter growth. As a result, shoot weights were similar after 4½ years for protected and unprotected trees. There was no evidence that treeshelters caused the trees to grow more shoots at the expense of roots since we found no differences in total root weights or shoot/root ratios between protected and unprotected plants.

We also could detect no differences in variables for plants provided different irrigation regimes. Although this finding suggests that normal rainfall is adequate to establish young oak seedlings, irrigation effects may have been masked by high moisture levels in the spring resulting from El Niño.

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Using Midday Stem Water Potential to Assess Irrigation Needs of Landscape Valley Oaks[1]

Ken Shackel[2] and Rob Gross[3]

Abstract

In a number of deciduous tree crops a reliable pressure chamber measurement of water stress (midday stem water potential or SWP) has been recently developed and found to be closely related to both irrigation regime and tree physiological responses to stress. A standard pressure chamber is used for the measurement of SWP, but prior to sampling, the leaf is enclosed in a reflective plastic bag and allowed to equilibrate with the water potential in the stem at the point of leaf attachment. In this study, measurements were made on valley oak trees under a variety of landscape conditions in Napa and Sonoma Counties, CA. Measurements on leaves that were only allowed to equilibrate for relatively short times (10 to 15 minutes) were compared to the SWP as measured by adjacent leaves that were allowed to equilibrate for over 1h. As found in other tree species, a 10- to 15-minute covering period appears sufficient in valley oaks for interior canopy shaded leaves to equilibrate with SWP. Using SWP in valley oaks that were nearby construction sites or agricultural land preparation, we confirmed that water stress was associated with root damage caused by these activities. SWP was also sensitive enough to follow the development of and the recovery from water stress over a number of irrigation cycles in an individual tree. We believe that SWP will be a valuable tool to determine the water needs of landscape valley oaks, particularly those with damaged root systems, while avoiding the potential for root disease development due to over-irrigation.

Introduction

Pressure chambers were designed to measure the water status of plants, and have been commercially available since the 1960s. However, the measurement of leaf water potential with the pressure chamber, especially at midday when water stress should be at it's maximum, has proven to be of little use in diagnosing water stress and scheduling irrigation. This is due to high measurement variability and an unclear relation of leaf water potential to plant physiological performance (e.g., Sinclair and Ludlow 1985). A more reliable pressure chamber measurement of water stress (midday stem water potential or SWP) was developed by McCutchan and Shackel (1992), and found for a number of tree crops to be closely related to both irrigation regime and to a range of physiological responses to stress such as reduced vegetative

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[1] An abbreviated version of this paper was presented at the Fifth Symposium on Oak Woodlands: Oaks in California's Landscape, October 22-25, San Diego, California.

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and fruit growth (Shackel and others 1997) and reduced stomatal opening (Shackel and others 1998).

Oak trees in the landscape are often subjected to stressful conditions such as soil compaction, prolonged drought, over irrigation or direct root damage, and these conditions may impair root health. Impaired root system health and function should lead to increased levels of tree water stress, hence an objective measure of water stress in oak trees may allow for the diagnosis and treatment of root system problems before appreciable decline occurs. The objectives of this study were to evaluate sampling protocols for the measurement of midday SWP in valley oaks *(Quercus lobata* Nee.) under field conditions and to determine whether SWP could reliably reflect changes in oak water stress associated with root damage and irrigation cycles.

Materials and Methods

The methods for sampling and measuring SWP have been previously described (McCutchan and Shackel 1992). Briefly, a lower canopy, shaded leaf, located near the trunk or a main scaffold branch, is enclosed in a reflective plastic envelope to suppress leaf transpiration for a sufficient amount of time to allow the water potential of the leaf to equilibrate with the water potential of the stem at the point of attachment (Begg and Turner 1970) and is called stem water potential (SWP). Equilibration periods of 1-2h are common (McCutchan and Shackel 1992). Since the water potential in the stem is determined by soil water availability, plant transpiration and root and stem resistance to water movement, SWP changes throughout the day and is typically lowest at midday (from about 1:00 pm to 3:00 pm).

In this study, measurements were made on valley oak trees under a variety of landscape conditions in Napa and Sonoma Counties, California. Measurements taken of leaves that were allowed to equilibrate for only 10 to 15 minutes were compared to the SWP as measured on adjacent leaves that were allowed to equilibrate for over 1h. Thirty trees were used for this comparison: 9 trees in a Yountville vineyard, 7 trees along the Lake County Highway in Calistoga, and 14 trees at Santa Rosa Junior College, 6 in an irrigated turf location (Burbank Auditorium) and 8 in a nearby unirrigated site (Bailey Field). A study was also conducted from 1997 to 1998 on five trees located in the Dominus vineyard in Yountville, California. The vineyard was supplementally irrigated with a single line per row drip irrigation system, but all oak trees were at least 12 ft. from the nearest irrigation point. All of the oak trees were located along an ephemeral stream bed that ran through the vineyard, but one was located near a construction site, and the roots of this tree had been severely damaged during various phases of construction *(table 1).*

On three occasions (October 7, 1997, June 3 and August 3, 1998), SWP was measured on all of the trees at the Yountville vineyard site. From August 3 to November 15, 1998, SWP was measured on tree number 2, which received three localized sprinkler irrigations during this period to minimize tree water stress. Weather data was obtained from a nearby California Irrigation and Information System (CIMIS) weather station (#77, Napa, CA), and was used to calculate a fully irrigated reference SWP value based on midday vapor pressure deficit. The approach was similar to that used by McCutchan and Shackel (1992), but in this case the values used were those developed for fully irrigated pear trees.[4]

Table 1—*Size, crown condition, and notes regarding location and root/soil conditions for five valley oak trees growing in a Yountville, California, vineyard that were monitored between October 7, 1997 and August 3, 1998.*

Tree No.	DBH (inches)	Crown rating (1 = Poor, 10 = Good)	Notes
1	47	3	Extensive construction related root damage, <50 ft. to the nearest vineyard irrigation line
2	39	2	Located at the edge of the stream bed, with many roots exposed by stream flow, 20 ft. to the nearest vineyard irrigation line
3	31	6	No apparent root disturbance, 15' to the nearest vineyard irrigation line
4	30	6	No apparent root disturbance, 12' to the nearest vineyard irrigation line
5	42	7	No apparent root disturbance, 18' to the nearest vineyard irrigation line

Results and Discussion

Measurements of SWP made on lower canopy, shaded leaves which had only equilibrated for about 10 to 15 minutes showed a significant correlation to adjacent leaves which had equilibrated for 1-2h *(fig. 1).* The slope and intercept of this regression were not statistically different from 1 and 0 respectively, and hence any equilibration time of 10 to 15 minutes or longer appears to be sufficient for the measurement of SWP in valley oak. In some cases the difference between adjacent leaves was substantial however, on the order of 0.5 MPa, and hence when an accurate estimate of an individual trees SWP is desired, it may be advisable to sample more than a single leaf per tree.

For the first three dates of sampling in the Yountville vineyard location, tree-to-tree variation was significant, with tree number 1, the root damaged tree, always showing the lowest SWP (most water stress), and tree number 5 generally showing the highest SWP *(table 2).*

These rankings in SWP were consistent with subjective crown ratings and the degree of root disturbance *(table 1),* with less vigorous crowns and more disturbed root systems generally associated with low SWP. It is interesting to note the consistency of tree ranking in SWP from October 7, when the soil profile was dry and SWP values were generally low, to June 3, when the soil profile had presumably not yet been depleted from the substantial winter rains of 1997/1998, and SWP values were both higher and with much smaller absolute differences in between trees. This indicates that impaired root health or impairment in other aspects of root water uptake may have chronic effects even under adequate soil water conditions.

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[4] Unpublished data: 1996 Research Reports of the California Pear Advisory Board.

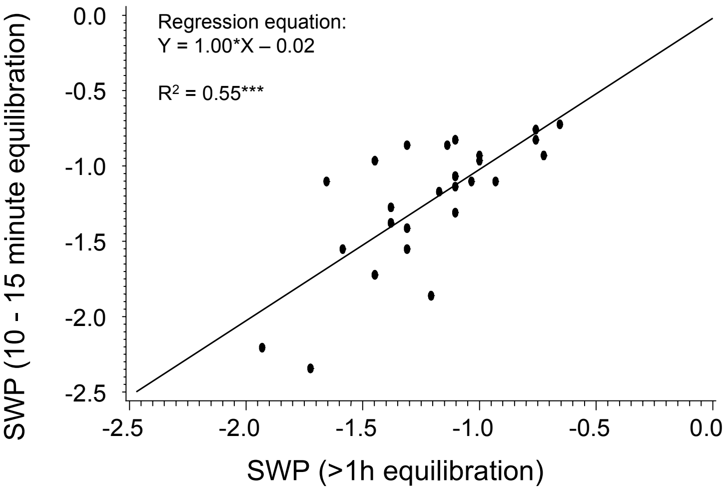

Figure 1—Comparison of midday stem water potential (SWP) measured on adjacent leaves with a short equilibration period (10 to 15 minutes, Y-axis), and a long equilibration period (>1h, X-axis). (*** denotes statistical significance of the regression at P<0.01).

Table 2—*Average SWP for individual trees on three dates in a vineyard in Yountville, California. Means followed by the same letter are not statistically different at the 5 percent level of Duncans new multiple range test. Means are from two to four leaves per tree on each sampling date.*

October 7, 1997		**June 3, 1998**		**August 3, 1998**	
Tree No.	SWP (MPa)	Tree No.	SWP (MPa)	Tree No.	SWP (MPa)
3	-1.04 a	5	-0.15 a	5	-0.83 a
5	-1.49 b	3	-0.17 ab	2	-0.87 ab
2	-1.84 c	4	-0.21 bc	3	-0.99 b
4	-1.86 c	2	-0.22 bc	4	-1.33 c
1	-2.29 d	1	-0.23 c	1	-1.85 d

In addition to comparisons among trees, for tree number 1 in the Yountville vineyard, SWP showed a consistent effect of sprinkler irrigation during the 1998 growing season *(fig. 2)*. Immediately following each irrigation, tree number 1 exhibited SWP values that were similar to those expected for a fully irrigated pear tree (typically about -0.7 MPa), but as time after irrigation increased, SWP progressively declined to values of between -1.5 and -1.8 MPa. These data indicate that, as found in other species of tree, SWP responds in a straightforward and sensitive manner to soil water availability, and hence should serve as a sensitive indicator of plant water status in oaks. If a suitable baseline or operational range of SWP can be established for oak trees, then this sensitivity should prove useful in deciding whether or not a particular tree, whose root system has been compromised by damage or disease, requires periodic supplemental irrigation to prevent excessive stress. Based on the tree with the best crown rating in this study (tree number 5, *table 1*), we can suggest that SWP values of about -1.5 by the end of the growing season may not represent excessive stress for oak trees, but this must be established with additional research. As in pears, SWP values on the order of -1.0 MPa or above appear to be associated with high soil water availability, and hence we can further suggest that any supplemental irrigation when oak SWP values are in this upper range may be considered unnecessary. Because both over- and under-irrigation can be determined by measuring SWP, we believe that SWP will be a valuable tool to insure adequate soil moisture of landscape valley oaks, particularly those with damaged root systems, without encouraging root disease development due to over-irrigation.

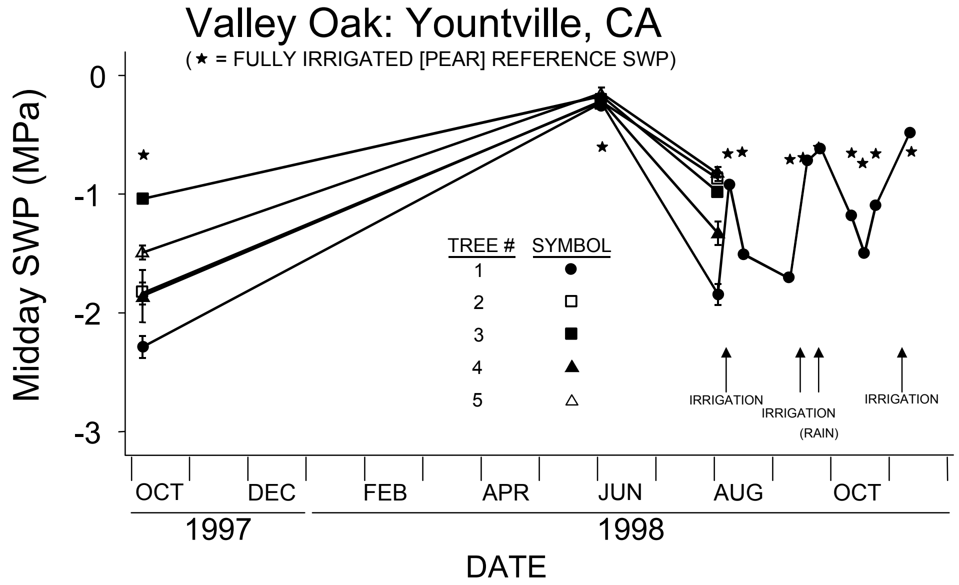

Figure 2—Midday SWP measured on five valley oak trees in 1997 and 1998, and for one of the trees (number 1), measured over three irrigation cycles in 1998. Also shown for reference are the SWP values expected for a fully irrigated pear tree under the same midday environmental conditions as the oaks.

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Geographic Patterns of Variation in Biomass Production of California Blue Oak Seedlings as a Response to Water Availability[1]

Susan Kloss[2] and Joe R. McBride[3]

Abstract

This study characterized the distribution of geographic variation in water relations traits for six populations of California blue oak along a precipitation gradient (two each from high, medium and low precipitation environments). Acorns were collected from each population, germinated and the resulting seedlings were experimentally treated with three different watering regimes in a greenhouse experiment. There were significant among-population differences in growth and biomass production characteristics in the seedlings. Significant among-treatment differences indicated at least low levels of plasticity, although there were no treatment x population interactions. Implications are that seed source zone maps should be used by restorationists until we have more information that coadapted or regional gene complexes do not exist.

Introduction

California's blue oak (*Quercus douglasii*) populations are found in areas that have historically received high levels of precipitation, as well as in much more arid areas. This study examined whether there are differences in seedling morphology among blue oak populations that reflect the action of natural selection on traits that respond to water availability. In this study, blue oak acorns were collected from six populations, germinated and cultivated in a greenhouse for one growing season, and subjected to three different watering treatments. The resulting effects on growth and biomass production of seedlings from each of the populations in each treatment were assessed.

Populations were different in latitude, longitude, elevation and average amount of precipitation received annually *(table 1)*. Multiple regression of ecological characteristics with means of plant morphological traits was used to assess whether among-population variation reflected the precipitation gradient, which would suggest that the two are linked. This study also suggested that there were significant

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[1] An abbreviated version of this paper was presented at the Fifth Symposium on Oak Woodlands: Oaks in California's Changing Landscape, October 22-25, 2001, San Diego, California.

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differences among these populations in traits whose means were significantly correlated with the water availability gradient in blue oak seedlings.

Table 1—*Locational and precipitation descriptions of the six blue oak populations included in the study.*

Pop	elevation (m)	latitude	longitude	30 yr precipitation normals (in)
1	325	40.40	122.25	60.80
5	150	40.18	122.06	28.07
6	725	39.26	121.16	66.17
16	600	37.59	120.22	31.55
23	150	37.02	119.37	13.77
25	800	35.42	118.47	18.73

California, because of the great variety of its climatic regimes and land forms, has more known biological diversity in its vascular plants, in terms of species richness, than any other state in the U.S. (Smith 1987). Many widespread species are not listed as threatened or endangered, but nonetheless, are losing the integrity of their gene pools, foreclosing evolutionary potential and resilience. Thoughtful planning could result in conservation of genetic diversity in these widespread species, preserving their evolutionary fitness by maintaining populations that have adaptations to local conditions. Knowledge of the factors that initiate and maintain patterns of variation are instrumental in establishing effective and efficient conservation practices (Hamrick and others 1991).

There is evidence that California's blue oak (*Quercus douglasii* H. & A.) populations are not regenerating at a rate that will maintain their current densities in certain areas of the state's oak woodland communities (Griffin 1971, Muick and Bartolome 1987). The apparent decline in the regeneration of blue oak has stimulated interest in conservation strategies for the species.

Information on geographic patterns of variation in blue oaks could be used to establish seed source zone maps. Establishing these maps could increase the long term success rate of planting and restoration projects by maintaining ecosystem integrity, since acorns from ecologically similar areas are more likely to produce blue oaks with necessary adaptations. Since blue oak is a keystone species, this may be important in the maintenance of ecosystem structure. In addition, delineation of seed collection zones will help maintain genetic integrity of populations and avoid the costs of rehabilitating the genetic diversity of a rare species, which can be prohibitive (Millar and Libby 1991).

Methodology

Maps of locations of six populations represented in common gardens established by McBride and others (1996) were overlaid with localities of California Cooperative Weather Stations. Statewide climatic data, stored at the National Climatic Data Center in Asheville, NC, were used to identify which of the fifteen Sierran populations represented in two common gardens have received high, middle, and low volumes of precipitation over a preceding 30 year period, based on weather information compiled between 1961 and 1991 by Owenby and Ezell for the National

Oceanic and Atmospheric Administration (NOAA 1992). Two populations from each of three precipitation patterns were selected (precipitation normals of approximately 60 inches, 30 inches, and 16 inches per year) (*fig. 1*).

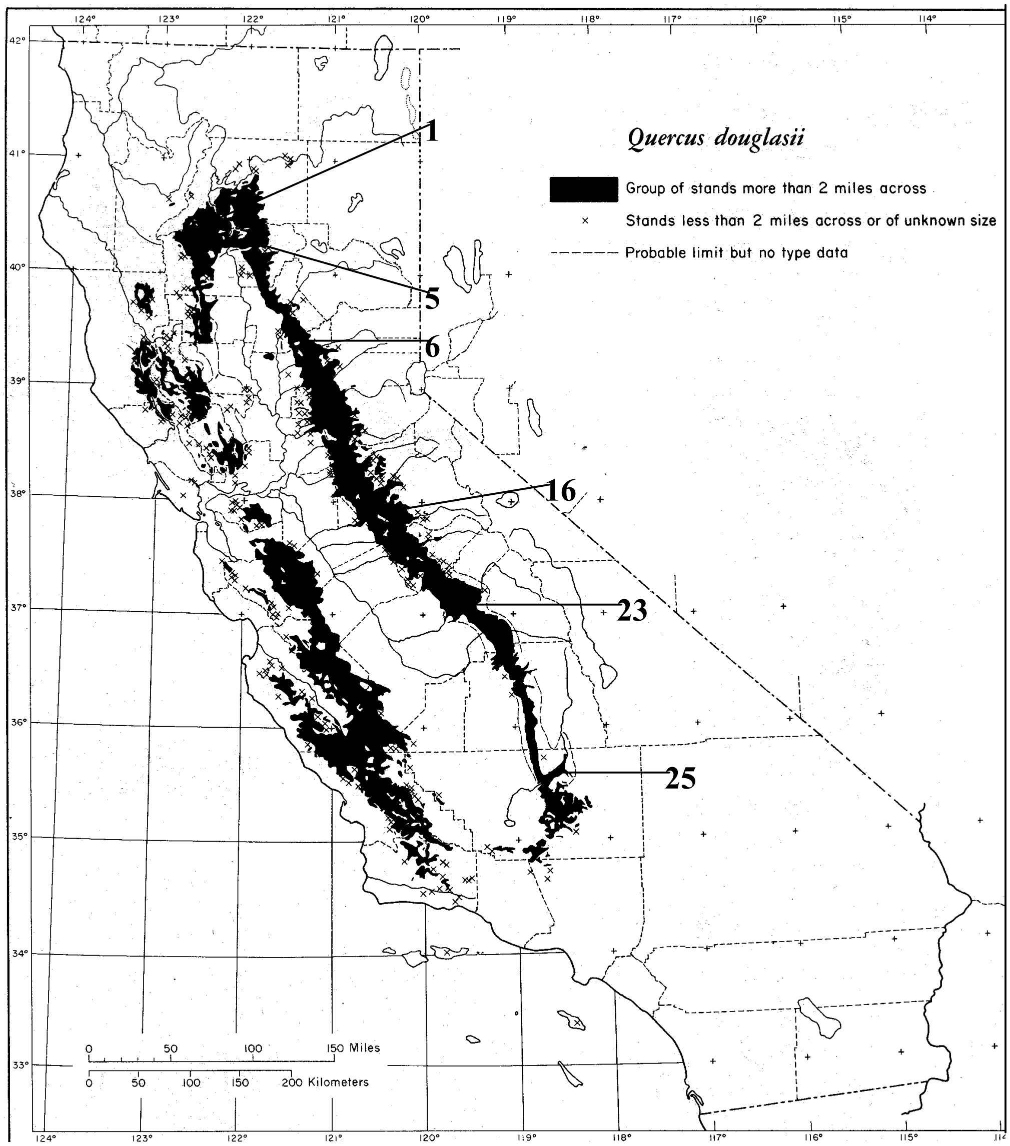

Figure 1—Map of blue oak populations included in this study, selected because of similarity and proximity to weather stations. (Adapted from Griffin and Critchfield 1972).

Acorns were collected from each of the six populations in October 1996. Ten trees, no closer than one hundred meters were selected in each population; approximately 100 acorns from each tree were gathered and bulked (McBride and others 1996). Acorns were dried to approximately 30 percent moisture content, placed on flats and refrigerated. Acorns remained in cold storage at approximately 36° F, until all populations reached 27 percent water content. The acorns were germinated in greenhouse flats in vermiculite. When most of the acorns from all populations had germinated, the germinated acorns were then randomly assigned and transplanted into individual containers.

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The acorns were germinated (emergence of the radicle) in greenhouse flats in vermiculite. Germination rate for all acorns was approximately 98 percent. As acorns germinated, they were returned to cold storage to inhibit growth until they were planted. When most of the acorns from all populations had germinated, the germinated acorns were then randomly selected, assigned and transplanted in pairs into individual containers similar in construction to milk cartons. Once shoots emerged, seedlings in all cartons were thinned by random selection so that each carton contained one seedling. Seedlings were randomly assigned a position on greenhouse tables. Containers were wrapped in aluminum foil, and were rotated in place and into different positions on the greenhouse tables on a weekly basis to minimize differential humidity, solar radiation and heating.

Thirty representatives from each of the six populations were randomly assigned to each of three different watering treatments. Treatments approximated soil water potentials expected in high (TH), medium (TM) and low (TL) precipitation environments from the range of blue oak. Seedlings were grown from February 1997 until bud set in October 1997.

Matric potential, the adhesive forces holding water to the surfaces of soil, is the predominant component of water potential in the soil. Matric potential was measured by inserting gypsum electrical resistance blocks into the soil and leaving them undisturbed for the length of the experiment. A subsample of pots, 10 per population, were fitted with gypsum block electrical resistance soil moisture sensors to monitor matric potential in the soil (an approximation of water availability) at 20 cm of depth.

In a study done by Evans and others (1975) at the Sierra Foothills Range Field Station owned by University of California, soil moisture was monitored over a 3-year period at 4, 8, 15, 30 and 45 cm below the soil surface, using both thermocouple psychrometers and electrical resistance blocks. Soil water potential at 15 cm generally fluctuated between –0.1 and –0.8 MPa, but occasionally reached –2.5 to –5.0 MPa at 30 cm of depth. These values were used to set treatment parameters for this study. Target levels of water stress were chosen to simulate natural environments, including the arid conditions experienced by some populations, without killing off the study seedlings. Target matric potential for the three treatments was reached when water potential in pots containing the gypsum blocks reached an average of –0.1 Mega Pascals (MPa) for TH, –0.7 MPa for TM, and –1.5 MPa for TL.

Soil moisture levels in containers with the electrical resistance blocks were monitored every other day from planting until bud set in the fall. When soil moisture reached target levels of matric potential in the containers with electrical resistance blocks, water was added to all the containers in a treatment until the soil reached field capacity.

At the end of the growing season, leaves were removed, soil was carefully washed from the root mass by placing the seedlings on a screen and rinsing them with a hose using a low-velocity water stream. Plants were separated into root and shoot portions at the air/soil interface. All biomass was oven dried for three days at 45ºC.

Data for growth and biomass production of greenhouse seedlings were analyzed by among-population differences, among-treatment differences, and population x treatment interactions. The dependent variables were: root biomass (g), shoot biomass (g), shoot height (cm), root:shoot biomass ratio, total leaf weight produced by the plant (g), total plant biomass production (shoot + root + leaves) (g), diameter of stem 1 cm from air/soil interface (mm), total number of leaves produced by the seedlings, and mean leaf weight (total leaf weight/total number of leaves/plant) (g).

The first assessment applied to the data collected in seedling biomass production was to correlate precipitation normals over 30 years with means of traits examined in this study. Next, analysis of variance was performed to determine whether differences among populations were statistically significant. Finally, Bonferroni post hoc tests would determine which population differences were statistically significant. This combination of assessments would describe the pattern of genetic variation in seedling growth and biomass production among populations of blue oak.

Results

Data were analyzed with a multiple regression model (SPSS 10.0© 1999).[4] Correlations significant at $p < 0.001$ were established among the three precipitation levels for the following variables: root weight, shoot height, shoot weight, total plant weight, stem diameter, and mean leaf weight *(table 2)*.

Table 2—*Greenhouse seedlings growth and biomass production and rainfall multiple regression correlations. Standardized coefficients and partial correlations suggested that rainfall was more highly correlated than elevation for all these variables.*

Trait	Significance (Pearson)		Partial correlations		Standardized coefficients (Beta)	
	rainfall	elevation	rainfall	elevation	rainfall	elevation
Root weight	0.000	0.013	0.132	-0.094	0.346	-0.208
Shoot weight	0.000	0.000	0.151	-0.144	0.395	-0.318
Root:shoot	0.055	0.000	-0.045	0.091	-0.119	0.206
Leaf weight	0.019	0.068	0.041	-0.040	0.112	-0.092
Tot. plant wt.	0.000	0.006	0.133	-0.101	0.348	-0.223
Shoot height	0.000	0.000	0.202	-0.191	0.531	-0.423
Stem diameter	0.000	0.001	0.078	-0.081	0.206	-0.180
Mean leaf weight	0.000	0.000	0.034	-0.043	0.086	-0.091

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[4] Mention of trade names or products is for information only and does not imply endorsement by the U.S. Department of Agriculture.

A multivariate general linear model (SPSS 10.0© 1999) found significant differences among populations and treatments for all variables (Pillai's Trace, Wilk's Lambda, Hotelling's Trace and Roy's Largest Root, all $p < 0.001$).

There was a significant effect of source populations for root weight, shoot weight, total plant weight, shoot height, stem diameter and mean leaf weight *(table 3)*.

Table 3—*Tests of between-subjects effects for blue oak seedlings growth and biomass production study.*

Source	Dependent variable	Type III sum of squares	df	Mean square	F	Sig.
POP	wtroot (g)	74.577	5	14.915	9.029	0.000
	wtshoot (g)	1.168	5	0.234	7.620	0.000
	r:s ratio	96.578	5	19.316	2.031	0.074
	leaf wt. (g)	2.151	5	0.430	6.931	0.000
	lf+rt+sht (g)	123.609	5	24.722	9.323	0.000
	shootht (cm)	432.041	5	86.408	6.272	0.000
	diam (mm)	6.201	5	1.240	4.634	0.000
	TOT LEAF	40.406	5	8.081	0.619	0.685
	mean lfwt	0.015	5	0.003	12.766	0.000
TMENT	wtroot (g)	24.163	2	12.082	7.313	0.001
	wtshoot (g)	0.426	2	0.213	6.952	0.001
	r:s ratio	73.370	2	36.685	3.858	0.022
	leaf wt. (g)	1.689	2	0.844	13.604	0.000
	lf+rt+sht (g)	46.601	2	23.300	8.787	0.000
	shootht (cm)	18.455	2	9.228	0.670	0.513
	diam (mm)	5.692	2	2.846	10.634	0.000
	TOT LEAF	353.671	2	176.836	13.550	0.000
	mean lfwt	0.001	2	0.000	1.125	0.326
POP * TMENT	wtroot (g)	9.272	10	0.927	0.561	0.845
	wtshoot (g)	0.185	10	1.851E-02	0.604	0.811
	r:s ratio	69.848	10	6.985	0.735	0.692
	leaf wt. (g)	0.677	10	6.767E-02	1.090	0.369
	lf+rt+sht (g)	15.717	10	1.572	0.593	0.820
	shootht (cm)	104.881	10	10.488	0.761	0.666
	diam (mm)	2.245	10	0.224	0.839	0.592
	TOT LEAF	101.852	10	10.185	0.780	0.648
	mean lfwt	0.001	10	0.000	0.569	0.839

In Bonferroni post hoc tests of among-population differences *(table 4),* root weight (g), shoot wt (g), shoot height (cm), total leaf weight produced by the plant (g), total plant biomass (leaf weight + root weight + shoot weight (g), stem diameter (mm), and mean leaf weight (total leaf weight/total number of leaves produced) all were significant at $p < 0.001$ *(table 3)*.

Table 4—*Among-population differences for blue oak seedlings. Growth and biomass production characteristics—all treatments combined.*[1]

Population	N	Root weight (g)	Shoot weight (g)	Root: Shoot ratio	Total leaf biomass (g)	Total plant weight (g) (leaves+root+shoot)	Shoot height (cm)	Stem diam. (mm)	Mean leaf weight (g)
1	87	4.38 (16,23,25)	0.459 (16,23,25)	10.51 (nsd)[2]	0.523 (16,23,25)	5.36 (16,23,25)	13.44 (16,25)	3.10 (25)	0.062 (16,23,25)
5	87	3.97 (25)	0.392 (25)	10.61 (nsd)	0.445 (25)	4.81 (25)	11.90 (nsd)	2.98 (25)	0.058 (16,23,25)
6	87	4.38 (16,23,25)	0.420 (25)	11.18 (nsd)	0.420 (25)	5.23 (16,25)	13.19 (25)	2.99 (25)	0.053 (1,25)
16	87	3.51 (1,6)	0.334 (1)	11.31 (nsd)	0.411 (1)	4.25 (1,6)	10.83 (1)	2.88 (nsd)	0.047 (1,5)
23	87	3.78 (1,6)	0.382 (1)	10.74 (nsd)	0.407 (1)	4.57 (25)	12.44 (25)	2.90 (nsd)	0.048 (1,5)
25	87	3.21 (1,5,6)	0.278 (1,5,16)	12.56 (nsd)	0.352 (1,5,6)	3.84 (1,5,6)	9.64 (1,6,23)	2.64 (1,5,6)	0.043 (1,5,6)

[1] Mean of population in cell followed by populations that are significantly different (Bonferroni, $p<0.05$)

[2] No significant differences between populations

For most traits where statistically significant differences among populations were observed, populations 1 and 6, which received at least 60 inches of rainfall normalized over 30 years, had the highest means in growth and biomass production characteristics, and population 25, with 30 year normals of 18.73 inches of rainfall had the least *(table 4)*. Significant traits included root weight, shoot weight (shown for example in *figure 2*), total plant weight (leaf + root + shoot), shoot height, and stem diameter.

The traits seedling height, stem diameter, root weight, shoot weight, mean leaf weight, total plant weight ($p < 0.001$) and total leaf biomass ($p = 0.019$) that were significantly correlated with 30 year precipitation normals indicated a strong relationship between seedling size and moisture availability. Root:Shoot ratio was not significantly correlated with 30 year precipitation normals *(table 2)*.

Tests of between-subject effects indicated significant between-treatment differences for all variables except shoot height and mean leaf weight *(table 3)*. Treatment differences in root weight, shoot weight, root:shoot ratio, total leaf weight, total plant weight, stem diameter, total number of leaves produced, and mean leaf weight were all statistically significant *(table 3)*. In general, the more water the plants received, the higher the growth and biomass production values. Conversely, root:shoot ratio generally became larger when plants received moderate or low watering treatments. Tests of between-subject effects for the population x treatment interaction term yielded no significant differences for any of the variables *(table 3)*.

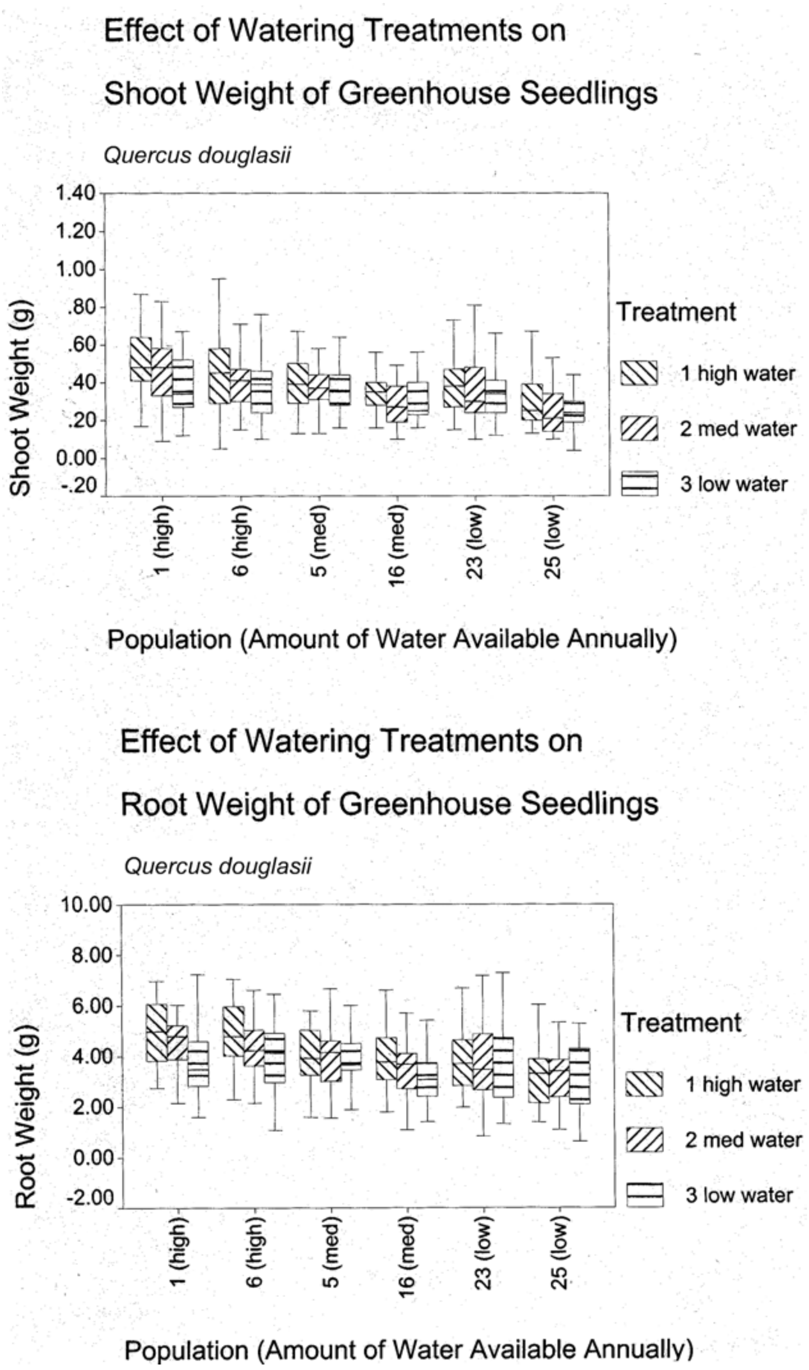

Figure 2—Plots of root weight and shoot weight for six populations of California blue oak (± range of sample).

Discussion

There were statistically significant differences among populations in growth and biomass production traits related to seedling size. Means of these traits were significantly related to water availability. Populations 1 and 6 were significantly different from populations 16, 23 and 25 for most of the traits that are significantly correlated with moisture availability. Analysis of the data suggested that seedlings from populations 1 and 6 have a higher relative growth rate than the other populations included in this study. Populations 1 and 6 are marginal populations which grow at the northern end of the range and receive as much as, or more water than other blue oak populations in California. Blue oaks in populations 1 and 6 often grow in woodlands and forests (closed canopy) where there are other tree species with which they must compete. In populations 23 and 25, in the southern end of the range, extra size does not confer any competitive advantage. There, blue oaks grow in savannas where trees are widely spaced. In those dry areas, few other tree species grow in blue oak habitat. In fact, when very low soil moisture is available, having to maintain excess biomass may be a competitive disadvantage because of the low water resources.

This study provided evidence to suggest that in general, blue oak seedlings have the ability to produce more biomass when more water is available but interaction plots did not show trends of populations responding to treatments differentially (statistically significant interactions), which would have provided evidence that particular populations respond differently to water availability (e.g. local adaptation in plasticity). The interaction plots for all variables showed consistent trends for all populations when compared across treatments. These findings indicate that plasticity in traits examined has not been selected for at the population level; i.e. the magnitude and direction of plasticity does not differ for some populations relative to others, for the soil moisture levels chosen for this study. There is difficulty in selecting levels of water stress that are high enough to force experimental seedlings to reveal adaptive traits without causing so much mortality that the research cannot be completed. Perhaps a study that has a range of levels of extreme water stress (perhaps the low end could begin at –1.5 MPa and the high end could be set at –3.0 MPa) may reveal adaptive traits or plasticity not detected in this study. Treatments of higher water stress could mimic natural selection by eliminating individuals that are not adapted to more extreme conditions of water stress.

Although this study specifically examined among-population differences related to the precipitation gradient in California blue oak habitat, it is likely that traits reflect a combination of environmental gradients as well as the water availability gradient. Maternal effects in blue oak have also been shown to be an important source of variation in acorn and seedling characteristics (Rice and others 1993). Analysis using a general linear model suggested that all populations for at least some of the traits had high levels of within-population variation, implying that there is variation either within or among individuals in a population, or both. This helps to explain the extensive range of blue oak and the varieties of climatic and community characteristics the species can endure.

Not all traits examined in the greenhouse study were correlated with water availability. This finding reflects the complexity of growth and biomass production in oaks, which is surely the result of combinations of many genetic and environmental factors, and their interactions. Elevation has a pronounced effect on length of the growing season. Plants at higher elevations are more subject to frost damage or mortality, and so generally have a restricted growing season relative to lower elevation plants. In addition, plants at higher elevations generally receive more precipitation than their counterparts at the same latitude but at lower elevations. Latitude, at least in an indirect manner, affects many factors including day length, temperature regimes, seasonal characteristics, and growth period as well as water availability.

In summary, there are significant differences among populations related to water availability in some seedling size and biomass production traits. However, other among population differences are likely to be diluted or indistinct in traits that result from interrelated environmental and genetic factors.

Conclusion

Seedlings of blue oak examined in this study exhibited ample variability in growth and biomass production traits within and among populations. This variability, in combination with the species' drought-avoidance and drought-tolerance processes, allows blue oak to be continuously distributed over such a broad expanse of area and ecological conditions in California. Blue oak seedlings demonstrated high within-population variability for many of the traits examined in this study, and significant among-population variability as well. Since seeds from the more mesic areas tended to yield seedlings that produced more biomass, perhaps seed source zone maps should be used for blue oak restoration or planting projects until evidence is produced that coadapted or regional gene complexes do not exist in this species.

Significant among-population differences existed in the variables root weight, shoot weight, leaf weight, total plant weight, shoot height, stem diameter and mean leaf weight. All these traits were significantly correlated with the water availability gradient. Because size of seedlings from populations 1 and 6 were significantly different from populations 16, 23 and 25 for most traits, these findings suggest that size may contribute to seedlings' ability to respond to high water availability.

The three treatments caused the means of each of these variables to differ significantly: Shoot weight, root weight, root:shoot ratio, leaf weight, total shoot weight, stem diameter, total number of leaves produced, although treatments did not cause significant differences in shoot height or mean leaf weight, probably because there was so much variation in each population.

The differences caused by treatments suggest that blue oaks have the ability to respond plastically, to some extent, to different levels of water availability. This finding is in agreement with Rice's finding of phenotypic plasticity in WUE of blue oak seedlings (1996).

Although traits that exhibited among-population differences were significantly correlated with the water availability gradient, it is likely that other environmental characteristics not examined in this study, such as temperature and day length, act in conjunction with water availability as selective forces. This study also did not assess the effects of combinations of environmental characteristics, for instance, temperature and precipitation, acting together. Further study in these areas would help continue to elucidate the geographic variation in populations of blue oak.

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Genetic Differentiation of Two California Red Oak Species, *Quercus parvula* var. *Shreveii* and *Q. wislizeni*, based on AFLP Genetic Markers[1]

Nasser Kashani[2] and Richard S. Dodd[3]

Abstract

Oaks are renowned for posing problems in defining species boundaries. One example is the case of the interior live oak complex that is usually taken to include two varieties of *Quercus wislizeni* from the Coast Ranges of California and the Sierra Nevada, and *Q. parvula* var. *shreveii* from the central coast of California. The latter taxon was separated from *Q. wislizeni*, and was recognized in *The Jepson Manual*, but still is not fully accepted, since its morphological separation is ambiguous. In an attempt to test differentiation of these two taxa, molecular genetic analysis was carried out using Amplified Fragment Length Polymorphism (AFLP) markers. A total of 202 individuals from 19 populations including *Q. parvula* var. *shreveii*, *Quercus wislizeni*, *Q. kelloggii* and *Q. agrifolia* were analyzed. Four primer sets generated 311 polymorphic band classes. Although species-specific markers were observed between *Q. kelloggii* and other members of the red oak group in California, fixed genetic differences were not apparent among *Q. agrifolia*, *Q. parvula* var. *shreveii* and *Q. wislizeni*. Cluster analysis and principal coordinate analysis revealed low levels of genetic differentiation among coast live oak, interior live oak and shreve oak. Cluster analysis also suggested that *Q. agrifolia* populations are more similar to populations of *Q. parvula* var. *shreveii* than to coastal populations of *Q. wislizeni*. This may reflect the relatively short time since divergence of these species. On the other hand, repetitive hybridization and introgression may have acted as a homogenizing factor for these genetic markers. The relatively high genetic similarity between *Q. agrifolia* and *Q. parvula* var. *shreveii* may have implications for the management of Sudden Oak Death in the limited range of the latter taxon.

Introduction

Characteristics such as high levels of phenotypic plasticity (Jensen 1988, Jensen and others 1984, Tucker 1974) and genetic variation (Guttman and Weight 1988, Hokanson and others 1993, Kremer and Petit 1993, Manos and Fairbrothers 1987, Samuel and others 1995, Schnabel and Hamrick 1990, Zanetto and others 1993) contribute to the success of the genus *Quercus*. However these features pose difficulties in estimating genetic differentiation between species, genetic architecture of populations, and definitive ruling on taxonomic relationship among species

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(Guttman and Weight 1988, Hokanson and others 1993, Manos and Fairbrothers 1987).

Studies on European white oaks (subgenus *Quercus*) show that most genetic variation is found within population rather than between populations or between species. Kremer and Petit (1993) reported that 74 percent of isoenzyme diversity is found within populations, whereas variation between populations and species are 3 percent and 23 percent respectively. Other studies on genetic variation of European and north American white oaks (Guttman and Weigt 1988, Muller-Starck and others1993, Schnabel and Hammrick 1990, Zanetto and others 1993) not only demonstrated that most genetic variation is found within populations, it also showed high genetic identity between populations and species.

There are approximately 200 species of red oaks (*Quercus*, section Lobatae) (Jensen 1997, Vazques and Nixon 1999) restricted to the New World. Jensen (1997) included 35 species of red oaks in "Flora of North America," north of Mexico.

Despite the rich diversity and wide distribution of red oaks in the U.S., relatively few molecular genetic studies have been conducted on their diversity and phylogeny. Similar to white oaks, most genetic variation in red oaks is contained within the population (though this level is higher for the red oaks, 98-99 percent than white oaks). Manos and Fairbrothers (1987) showed low estimates of genetic diversity between populations (Dst= 0.001-0.021) as compared to within population diversity (HS= 0.055-0.115) in red oaks of New Jersey. They further showed minimal differentiation among five of the six species studied. In a similar study over a wide range and multiple species of subgenus Lobatae, Guttman and Weigt (1989) found most red oak taxa to be similar in mean number of alleles per locus, percent polymorphic loci and mean heterozygosity. Schwarzman and Gerhold (1991) and Hokanson and others (1993) also reported low levels of genetic differentiation among populations and between species. Hokanson and others (1993) further found no species-specific markers for *Q. rubra* and *Q. ellipsoidalis* from the Apostle Islands, Wisconsin, despite high levels of polymorphism among the enzymes studied.

Studies on genetic variation or genetic differentiation of California red oaks are very limited (Dodd and others 1993a, Dodd and others 1993b, Dodd and others 1997, Millar and others 1990). Univariate and multivariate analysis of acorn fatty acids of *Q. agrifolia* and *Q. wislizeni* [classical name of *Q. wislizeni*i is changed to *Q. wislizeni* according to the new International Code of Botanical Nomenclature (Greuter 1994)] significantly separated these two species from each other ($p<0.0001$) (Dodd and others 1993). Among fatty acids identified, oleic acid and the percentage of unsaturated fatty acids were significantly higher in *Q. agrifolia* than in *Q. wislizeni*.

In a recent study, Dodd and others (1997) showed marked biochemical differences between *Q. wislizeni* from the Sierra Nevada and a population of *Q. parvula* from Palo Colorado canyon on the Central coast of California (type locality for *Q. parvula*). Sierran populations of *Q. wislizeni* showed low levels of the aliphatic hydrocarbon hentriacontane (C29) while this pattern was reversed in populations of *Q. parvula*. This pattern was not very clear in coastal populations of *Q. wislizeni*, as they were more variable and includes individuals with *Q. parvula* biochemical characteristics. Dodd and others (1997) suggested that the variable pattern observed in the coastal populations of *Q. wislizeni* might be result of hybridization between *Q. wislizeni* and *Q. parvula*.

In view of morphological and chemical data supporting the differentiation of *Q. parvula* and *Q. wislizeni*, it was considered important to search for molecular genetic evidence (Amplified Fragment Length Polymorphism, AFLP markers) to substantiate species status and also to investigate the possible range of *Q. parvula*. Further, the genetic relationship of these taxa with other California black oaks (*Q. agrifolia* and *Q. kelloggii*) will be examined.

Materials and Methods

Experimental Material

Foliage was collected from 6-10 individuals from each of 11 populations of *Q. wislizeni* var. *wislizeni* and 4 populations of *Q. parvula* var. *shreveii* (hereinafter referred to as *Q. parvula*). The shrub form of *Q. parvula* was not considered in this analysis. Sampled individuals of the former species included 6 populations from the foothills of the Sierra Nevada and 5 populations from the coast ranges of California (*table 1, fig. 1*). Putative hybrid individuals were sampled if they were encountered in the population. Two control populations each of *Q. kelloggii* and *Q. agrifolia* were added to the analysis. These controls were collected from presumed pure populations (*table 1*, *fig. 1).* Within each population, foliage from mature trees at least 50 m. apart were collected randomly. Leaves were kept on ice and subsequently at 4ºC until extraction.

Table 1—Location of populations sampled.

Pop code	Species	Location	County	Nearest city	Latitude	Longitude
W07	*Q. wislizeni*	Brickyard Rd. (Hwy 88)	Amador	Ione	32° 21′	120° 55′
W53 (K53)	*Q. wislizeni* [1,2]	Geysers Rd.	Sonoma	Geyserville	38° 45′	122° 50′
W55 (K55)	*Q. wislizeni* [1,2]	Orr Springs Rd.	Mendocino	Ukiah	39° 11′	123° 16′
W60 (K60)	*Q. wislizeni* [2]	Covelo Rd. (Hwy 162)	Mendocino	Longvale	39° 34′	123° 25′
W66 (K66)	*Q. wislizeni* [1,2]	Highway 70	Butte	Oroville	39° 38′	121° 33′
W67	*Q. wislizeni*	Highway 36	Tehama	Red Bluff	40° 20′	122° 06′
W68 (K68)	*Q. wislizeni* [1,2]	Lake Shasta (Bailey Cove)	Shasta	Redding	40° 49′	122° 18′
W69 (K69)	*Q. wislizeni* [2]	Highway 299	Shasta	Whiskey Town	40° 37′	122° 31′
W70 (K70)	*Q. wislizeni* [1,2]	Highway 3	Trinity	Douglas City	40° 37′	122° 57′
W72	*Q. wislizeni*	Highway 140	Mariposa	Midpines	37° 33′	120° 24′
W75	*Q. wislizeni*	Highway 4	Calaveras	Copperopolis	37° 59′	120° 39′
P71	*Q. parvula*	Big Creek reserve	Monterey	Lucia	36° 05′	121° 36′
P73	*Q. parvula*	Sycamore Canyon Rd.	Monterey	Big Sur	36° 13′	121° 47′
P78	*Q. parvula* [1]	Nacimiento-Fergusson Rd.	Monterey	Lucia	35° 09′	121° 28′
P79	*Q. parvula*	Coast Rd.	Monterey	Big Sur	36° 17′	121° 51′
K01	*Q. kelloggii*	Blodgett Reserve	Placer	Georgetown	38° 56′	120° 43′
K74	*Q. kelloggii*	Highway 299	Humboldt	Blue Lake	40° 54′	123° 55′
A03	*Q. agrifolia*	Marshall-Petaluma Rd.	Sonoma	Marshall	38° 10′	122° 54′
A04	*Q. agrifolia*	Petaluma-Point Reyes Rd.	Sonoma	Point Reyes Station	38° 05′	122° 48′

[1] Population where putative hybrids were observed and collected.

[2] Population where *Q. kelloggii* was collected in addition to target species. Code in parenthesis

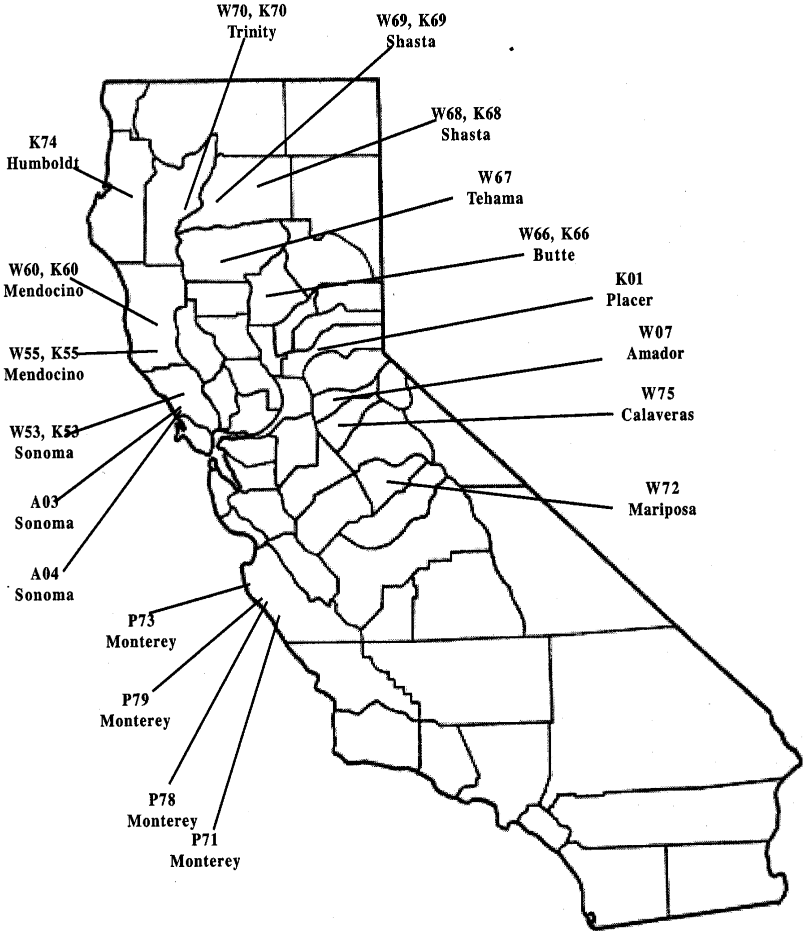

Figure 1—Map of sampled populations in California by county. (For more detail on locations see *table 1).*

DNA Extraction and AFLP Procedure

DNA was extracted from fresh foliage following a simplified Doyle and Doyle method (Cullings 1992). The amplified fragment length polymorphism (AFLP) method of Vos and others (1995) was performed following the protocol of Life Technologies (Rockville, MD, U.S.A.). DNA was restricted with *Eco*RI and *Mse*I (1.25 U/µl of each) in a reaction buffer [10 mM tris-HCl (pH 7.5), 10 mM Mg-acetate and 50 mM K-acetate] in a total volume of 12.5 µl. The restriction reaction was carried out at 37°C for 2 hours followed by denaturation of restriction enzymes at 65°C for 10 min. Adapter ligation was conducted in the ligation buffer using T4 DNA ligase for 2 hours at 20°C. Subsequently, the ligation product was diluted 1:10 for primary amplification.

Primary amplification was carried out in a standard Polymerase Chain Reaction (PCR) cocktail containing 1.5 mM MgCl2 and 0.5 mM of each of the primary amplification primers. For the primers, the EcoRI primer sequence was identical to the adapter sequence, whereas the MseI primer had an extra cytosine ("C") as a selective nucleotide *(table 2).* The PCR reaction was performed in a Techne Genius thermocycler for 20 cycles using the following cycling parameters: 30 s at 94°C, 60 s at 56°C and 60 s at 72°C. The primary amplification product was then diluted 1:50 for selective amplification. Selective amplification was carried out in a standard PCR reaction cocktail containing 2.5 mM MgCl2 and 0.5 mM of the selective amplification primers. The PCR program had two cycles: 13 cycles of 30s at 94°C, 30 s at 65°C (annealing temperature was lowered 0.7°C at each cycle) and 60 s at 72°C, followed by 23 cycles of 30 s at 94°C, 30s at 56°C and 60 s at 72°C. Four sets of selective primers were used: 1/2, 3/5, 3/6 and 4/8. Selective amplification products were resolved on 6 percent polyacrylamide native gel. Gels were stained with Gelstar (FMC Bioproducts, Rockland, ME, U.S.A.) following manufacturer protocol and documented with a Kodak DC 120 digital camera. Bands were scored as present/absent using Gelcompar II software (Applied Maths, Kortrijk, Belgium).[4]

Statistical Analysis

AFLP scores were treated phenetically and any reference to genetics (e.g. molecular genetic markers) implies observed restriction length variation as revealed by AFLP methodology. UPGMA (Un-weighted pair-group method using arithmetic averages) cluster analysis (Sneath and Sokal 1973) was carried out on Jaccard's coefficient (Dunn and Everitt 1982). This coefficient is the ratio of number of positive matches to the total number of characters minus the number of negative matches. Jaccard's coefficient omits consideration of negative matches (Sneath and Sokal 1973). Cluster analysis is a process in which samples are partitioned into one or more groups (clusters) in a hierarchical order. UPGMA in particular calculats the average similarity or dissimilarity of a candidate sample to an extant cluster. Principal coordinate analysis and cluster analysis were carried out using NTSYS-pc (Rholf 1993). Principal coordinate analysis is an ordination method in which samples are grouped together based on their similarities. The output of the analysis usually is plotted on a two dimensional graph, which help the researcher to inspect the possible relationship of the samples or specimens.

Results

Four primer sets generated a total of 311 band classes for all the individuals in the study, including putative hybrids. *Q. kelloggii* showed the least number of band classes followed by *Q. agrifolia*. Several markers also were observed to be fixed for *Q. kelloggii*. Principal coordinate analysis (Pcoor) of all individuals of *Q. agrifolia*, *Q. kelloggii*, *Q.* parvula and *Q. wislizeni* showed clear separation of *Q. kelloggii* from other red oaks of California (*fig. 2*). The remaining species showed three overlapping groups. Both *Q. parvula* and *Q. wislizeni* showed high variability, as it is evident by the spread of individuals of these species on Pcoor plot (*fig. 2*). This could have arised from wider range of sampling for *Q. parvula* and *Q. wislizeni*, while *Q. agrifolia* populations were apart not more than 20 miles. However *Q. kelloggii* populations which were sampled over wide range showed a very close affinity to each other. UPGMA of all individuals was in agreement with the principal coordinate analysis (*fig. 3*). Two major clusters were observed. All black oak individuals fell in

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[4] Mention of trade names or products is for information only and does not imply endorsement by the U.S. Department of Agriculture.

one cluster and individuals of each population shared a common node. The second major cluster contained *Q. agrifolia*, *Q. parvula* and *Q. wislizeni*. Individuals of each population of coast live oak shared a common node, while individuals of shreve oak populations did not always branch from the same node. For example, individuals of population P71 branched from two different nodes. Except for the populations W07 and P71 which clustered with *Q. agrifolia* populations in the second major cluster, all other populations of *Q. parvula* and *Q. wislizeni* shared a common node. Similar to shreve oak, all individuals of some populations of interior live oak shared a common node while others (W53, W60, W66, W68 and W70) branched from different nodes. In this analysis, one *Q. agrifolia* and several *Q. parvula* and *Q. wislizeni* did not resolve with their respective populations and placed as basal branches to the dendrogram (unresolved). UPGMA of all individuals of *Q. parvula* and *Q. wislizeni* showed no major changes in the topology compared to previous analysis (data not shown). However, four individuals of population W69 clustered with population P71 and W07.

Lack of clear resolution of some individuals under study into their respective clusters or groups could have come from misidentification of bands. This could have occurred either at band selection or band class grouping stages. At the band selection stage, a band could have been misidentified either due to its weak signal or being obscured by a strong signal from an adjacent band. Band class grouping was performed by the "Gelcompar" algorithm and was set to minimize misclassification. Failure to identify a band (band selection) or misclassification of a band to a different class could potentially cause distortion of the data. To minimize this effect, a population was considered as an operational taxonomic unit (OTU). For these OTUs, a character (band class) was accepted as being present, if at least one individual of a population carried the band. Similarly, a band was considered missing when the marker was absent in all individuals of the population. Then UPGMA based on OTUs was performed. The resulting dendrogram consisted of 2 major clusters, the *Q. kelloggii* cluster and the cluster of all other live oak OTUs *(fig. 4)*. This dendrogram also supported high phenetic similarity of coast live oak, interior live oak and shreve oak.

Discussion

The observed levels of taxon differentiation in genus *Quercus* varies depending on the choice of characters (Bruschi and others 2000, Chechowitz and others 1989, Hokanson and others 1993, Le Corre and others 1997). Based on morphological and biochemical characters, oaks can be separated into distinct species (Bruschi and others 2000, Dodd and others 1996,). However, allozyme (direct product of genes) and nuclear genome markers (e.g., RFLP, RAPD and AFLP) have frequently failed to allow clear resolution of species boundaries between closely related oaks (Schwarzman and Gerhold 1991, Le Corre and others 1997, Bruschi and others 2000). *Quercus parvula* and *Q. wislizeni* are not exceptions to this.

Using 16 quantitative and 14 subjectively scored morphological characters; Nixon (1980) clearly separated *Q. parvula* and *Q. wislizeni* from each other. However, his data failed to resolve the varieties of these species as separate groups. In the present study, AFLP markers fail to place all *Q. parvula* and *Q. wislizeni* populations into two separate clusters. However, *Q. parvula* populations P78, P79 and P73 constituted their own cluster except for P732 and not exclusive of W712 and

W536. Individuals of population P71 shared a common node. The latter (P71) is in the same cluster with W07 and some individuals from W69 as well as W723 and P732. The former populations (P78, P79, and P73) are in the same cluster as W75. Lack of clear resolution of red oak taxa into distinct groups (clusters) based on AFLP markers is consistent with other molecular genetic studies of red oaks (Manos and Fairbrothers 1987, Guttman and Wiegt 1989, Hokanson and others 1993). Manos and Fairbrothers (1987) and Guttman and Wiegt (1989) found no species-specific marker of any value for identifying most of the red oak species that they studied. The present study also demonstrated lack of species-specific markers among the evergreen oak species studied. Except for absence of several AFLP markers in *Q. kelloggii*, no species-specific marker could be found among these oaks. Moreover, several markers were fixed or nearly fixed for the California black oak, while no fixed markers were observed for the other species. Manos and Fairbrother (1987) and Guttman and Wiegt (1988) suggested the relatively short time since divergence and rapid speciation as causes for scarcity of molecular genetic markers in red oaks of the eastern United States.

In late Eocene strata, fossil foliage of species displaying characteristics of major groups of oaks (e.g., subgenus Lobatae) has been found. In the Miocene (5-13 mya) most oak species existing today were evidently present (Wolfe 1979). Fossils of *Q. kelloggii* ancestors were reported from the early Miocene fossil flora of California while the progenitor of *Q. wislizeni* and *Q. agrifolia* was described from the late Miocene fossil flora. Nixon (1980) postulated that the nearest relatives of a *Q. parvula* progenitor are likely to found in central and southern Mexico, while ancestors of *Q. wislizeni* probably had close affinities to interior desert species of northern Mexico. Nixon (1980) suggested that the progenitor of *Q. parvula* was associated with "oak-pine-laurel" forest of the Tertiary and was restricted to the subtropical coastal forests of California. Nixon (1980) also suggested that the *Q. wislizeni* ancestor was found in interior woodland and savannah habitats. Alternatively, Axelrod (1983) proposed a common ancestor for interior live oak and shreve oak. Axelrod (1983) estimated that about 20 mya shrevoides, a progenitor of *Q. parvula*, first appeared in west-central Nevada and shifted westward to the Sierra Nevada. As climate became dryer in the Upper Miocene (13-12 mya), wislizenoides replaced shrevoides, at first in western Nevada, and later in the lower Sierra Nevada and the Inner Coast Ranges. According to Axelrod (1983), the *shreveii* line has contributed to mesic broad-leaved sclerophyll forest for fully 18.5 million years. *Q.* wislizenoides, on the other hand, has typified semiarid oak-grassland and woodland vegetation since the later Miocene. Axelrod (1983) further postulated that oaks of the *wislizeni* alliance are related to series Peninsulares of Baja California, which in turn is associated with series Durifokiae of the southwestern United States and northwestern Mexico.

Results of the present study are more easily reconciled with Axelrod's (1983) hypothesis of a common progenitor for *Q. parvula* and *Q. wislizeni* than with Nixon's (1980) idea. Both cluster analysis and principal coordinate analysis showed a high degree of similarity between these two species *(figs. 6-12)*. Even though most *Q. parvula* populations shared a common dendrogram node, these populations were scattered within the same major cluster containing *Q. wislizeni*. Principal coordinate analysis of *Q. wislizeni* and *Q. parvula* also showed a close affinity between interior live oak and shreve oak, and was not able to segregate these two species into distinct groups. As in eastern red oaks (Guttman and Weigt 1989, Manos and Fairbrothers

1987), rapid speciation with minimal changes in AFLP markers may have occurred since divergence of *Q. parvula* and *Q. wislizeni* about 10-15 mya (Axelrod 1983).

The high similarity between *Q. parvula* , *Q. wislizeni* and *Q. agrifolia* could be explained by reticulation of characters due to frequent hybridization. It is plausible that during the last glaciation in late Pleistocene the distribution of California red oaks was constricted to refugia on the central and southern slopes of the coast ranges and western slopes of the southern Sierra Nevada. In these refugia, extensive hybridization and introgression conceivably could have occurred. After retreat of the glaciers, oaks may have expanded in distribution rapidly with minimal changes in AFLP neutral markers. However if this is the case, *Q. kelloggii*, which hybridizes with each of the evergreen oaks of California, should have shown a higher degree of similarity with other red oaks in this study. All the analyses showed a clear separation between *Q. kelloggii* and other red oaks. It is very difficult to assume absence of *Q. kelloggii* from these putative refugia; but uni-directional gene flow from California black oak to other evergreen red oaks could have occurred. Evidence of hybridization in black oaks of California will be discussed in Chapter 3.

The current study showed strong similarity among *Q. agrifolia*, *Q. parvula* and *Q. wislizeni*. However, Muller (1938) noted close affinity between *Q. parvula* and *Q. agrifolia*. He placed these species in the section Agrifolae, which includes *Q. wislizeni*. Considering the small number of coast live oaks used in this study, it is very difficult to draw any definitive conclusion about the genetic relationship of *Q. agrifolia* with *Q. parvula* and *Q. wislizeni* or the progenitor of *Q. agrifolia*. Nevertheless, it is possible that *Q. agrifolia* may have evolved from a *Q. parvula* like progenitor. Sampling more *Q. agrifolia* probably will show more genetic variation and possibly more separation between coast live oak and the other taxa.

Conclusion

The current study showed no diagnostic AFLP markers that would allow unequivocal discrimination between *Q. parvula* and *Q. wislizeni*. However, fossil records (Axelrod 1983) ecological preferences (Nixon 1980, Tucker 1997) and biochemical data (Dodd and others 1997) furnish enough evidence to consider these taxa as two separate species. Radiation over a relatively short time period, and rapid morphological divergence with minimal changes in nuclear genetic markers [e.g., allozyme (Millar and others 1990), AFLP (current study)] may provide the best explanation for the high similarity observed between shreve oak and interior live oak. Even though convergence of characters due to hybridization cannot be ruled out, the evidence presented here suggests a common progenitor for *Q. parvula* and *Q. wislizeni* (Axelrod 1983) and possibly *Q. agrifolia*. Unless a thorough phylogenetic analysis based on nuclear and organellar DNA sequences are conducted, the taxonomic status of *Q. parvula* and *Q. wislizeni* cannot be settled with confidence.

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Mating Patterns in a Savanna Population of Valley Oak (*Quercus lobata* Neé)[1]

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Abstract

California valley oak is threatened by landscape alteration and failing recruitment in remnant stands. Its reproductive ecology is a key element of the seedling recruitment process. We first examine the mating system, to determine the extent of inbreeding in a population at Sedgwick Reserve, in Santa Barbara County. We then quantify variation in germination success and acorn size, evaluating their spatial patterns across the site. We collected acorns from 21 mapped focal trees in fall 1999, measured their average seed weight and germination success, and identified their multilocus genotypes. Using a mixed mating model, we observed significant, but modest selfing (outcrossing rate: $t_m = 0.96$) and no mating among relatives ($t_m - t_s$) = 0.0. The effective pollen donor number was estimated to be between 5 and 7 individuals, depending on the inbreeding coefficient of the adults. These mating results indicate relatively little inbreeding but low numbers of pollen donors. Mothers differed significantly in seed weight (range: ~ 4 - 10 g) and germination percentage (range: 0 – 90 percent), and a bivariate analysis showed a gradient across the study site. Such a pattern suggests that environment conditions influence acorn size and germination success. Future work will address whether isolated individuals are at risk of selfing, for the expression of inbreeding depression on seed traits, or a reduction in the effective pollen donor number.

Introduction

Valley oak (*Quercus lobata* Neé) is one of California's most distinctive oak species. Its massive size and majestic canopy, combined with its longevity, make it a signature element of California's foothills, valleys and floodplains. Unfortunately, land use changes and restricted recruitment within remnant stands have caused its steady decline for 200 years (Adams and others 1992, Bolsinger 1988, Brown and Davis 1991, Griffin 1971). Because the species prefers level, fertile sites that are valuable for agricultural and development purposes, valley oak will continue to be vulnerable to the impact of land conversion. Numerous studies have estimated the losses thus far and predicted future declines (Bolsinger 1988, Brown and Davis 1991, Davis and others 1998, Greenwood and others 1993). Knapp and others (2001) recently reported reduced acorn production in blue oak (*Quercus douglasii*) trees

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with few local neighbors, and concluded that reduced pollen flow to isolated individuals might be the cause. If low adult density reduces acorn production in oaks, then progressive demographic attrition and stand thinning may jeopardize recruitment, through reduced acorn availability. However, before we can determine whether valley oak may be reproductively vulnerable, we need more information about the mating system of this species.

The mating system of a plant can be summarized with estimates of the outcrossing rate, mating with relatives, and probability of two progeny having the same mother and father (Ritland 1983, 1990; Ritland and Jain 1981). Such information is helpful, because it provides an indication of the extent of inbreeding allowed by the mating process. For species with a history of outcrossing, typical of most tree species, inbreeding can lead to inbreeding depression, expressed through reduced seed set or progeny fitness (Ellstrand and Elam 1993). In addition, information about the probability that two progeny share the same father can reveal the extent of diversity in pollen donor pool and can provide an indicator of the effective number of pollen donors for a given maternal plant (Ritland 1989). For outcrossing species, the effective number of donors may be a more sensitive indicator of mating than the outcrossing rate per se. It takes only one other tree to ensure outcrossing, but from an evolutionary perspective, it is critical to know whether that outcrossing represents few or many other individuals. Moreover, because mating system parameters are relatively easy to estimate, this information can be gathered for several sites to facilitate comparison among populations occupying different sorts of landscapes (Sork and others 1999).

The possibility that valley oak adults may be at risk for reproductive isolation has been addressed elsewhere through a study of pollen movement at Sedgwick Reserve, Santa Barbara Co. (Sork and others 2002). That study used a novel analytical method, dubbed TwoGener (Smouse 1998, Smouse and others 2001), which combines the two-generation gametic inference of parentage analysis (e.g., Chakraborty and others 1988, Devlin and others 1988) with the survey methods of population structure analysis. With TwoGener, we can estimate not only the effective number of pollen donors in a mating neighborhood (N_{ep}), but also the average distance of successful pollen movement (δ). With certain assumptions, we can estimate the decay parameter of the pollen dispersal curve and can then deploy that curve to describe landscape-scale patterns of pollen movement for geo-referenced individuals (Austerlitz and Smouse 2001). Our analysis of the data available to date has yielded a surprisingly small estimate of the effective number of pollinators, N_{ep} = 3.68 individuals, and an estimated average distance of successful pollination of δ = 64.8 m (Sork and others 2002). The effective pollen donor values are much lower than those observed for wind-pollinated species in closed-forest settings in Missouri Ozark forests. For white oak (*Quercus alba*), we estimate that $N_{ep} \sim 8$ individuals and $\delta = 11$ m (Smouse and others 2001); for shortleaf pine (*Pinus echinata*), we estimate that $N_{ep} \sim 10$ individuals (extracted from Dyer and Sork 2001). Although the pollen dispersal estimate is higher for valley oak than for either of these closed-forest canopy species, we had anticipated an even longer average successful pollination distance, given the savanna setting of our population. Interestingly, the scale of pollination distance observed in valley oak is comparable to the 60-meter scale at which Knapp and others (2001) observed an association between reduced acorn crop size and small numbers of near neighbors in *Q. douglasii*. Both the Blue oak (Knapp and others 2001) and valley oak (Sork and others 2002) results point to the need for a better understanding of mating patterns in California savanna-oak settings.

The first objective of this paper is to evaluate the mating system of the Sedgwick Reserve population of valley oak, through Ritland's MLTR program (1990), using those same first year data from our pollen movement study (Sork and others 2002). Ritland's approach provides a population estimate of the extent of inbreeding (through selfing and mating between relatives) and it also provides a separate estimate of the effective number of pollen donors, which latter can be compared with a corresponding estimate, independently available from TwoGener. The data reported here are from one site and one year, but they represent an initial step toward a larger understanding of variation in mating patterns of valley oak populations across different landscapes, and the extent to which those processes are contributing to the ongoing recruitment challenge for threatened populations. Eventually, successful management of valley oak will require an approach that allows us to compare not only populations, but also individual trees, using specific information about the spatial locations of near neighbors and local tree density. We will use the results of this study to seed a discussion of future directions for our enquiries.

The second objective is to report findings on two fitness-related components of the reproductive biology of valley oak: seed size and germination success. Germination success is key to seedling recruitment, and seed size is often associated with early seedling survival and height growth. Inbreeding depression can have negative impact on either trait (Ellstrand and Elam 1993), even though maternal genotype and maternal environment can have a large influence on successful seedling establishment. As an initial inquiry into these two fitness-related components of valley oak recruitment, we quantify the extent of their variation among study trees, and we assess whether the variation is distributed randomly across the landscape. A nonrandom spatial distribution can indicate either the genetic consequences of restricted gene flow or the spatial pattern of environmental effects. For example, with restricted gene flow, adjacent (related) trees may have similar reproductive traits. Alternatively, spatial pattern in these traits may indicate the impact of environmental gradients. Our motivation for this analysis is to determine whether there are spatial patterns in the features determining recruitment success, which can then be pursued in future studies. Because density also varies within our site and density may affect inbreeding, we include this factor in our analysis of seed size and germination.

Materials and Methods

Study Site

We conducted our work at the Sedgwick Reserve, along the valley floor of Figueroa Canyon (N 34°42', W 120° 2'), 10 km northeast of Santa Ynez, California. Sedgwick Reserve is a 2,380 ha area, managed for research, education and conservation of native biodiversity by the University of California Natural Reserve System and UC Santa Barbara. The study trees in Figueroa Canyon are located on the valley floor and surrounding hill slopes in a broad, shallow basin, roughly 130 ha in extent and ranging in elevation from 360 m to 405 m above sea level. In fall 1999, we selected 21 reproductive valley oak adults at the study site, arrayed in an approximate hexagon-shaped grid, with six triangular clusters (three trees each) at the six vertices of the hexagon, and one in the middle (*fig. 1*). The inter-female distances within each cluster ranged from about 50-150 m; the maximum distance across the hexagon was 1,040 m.

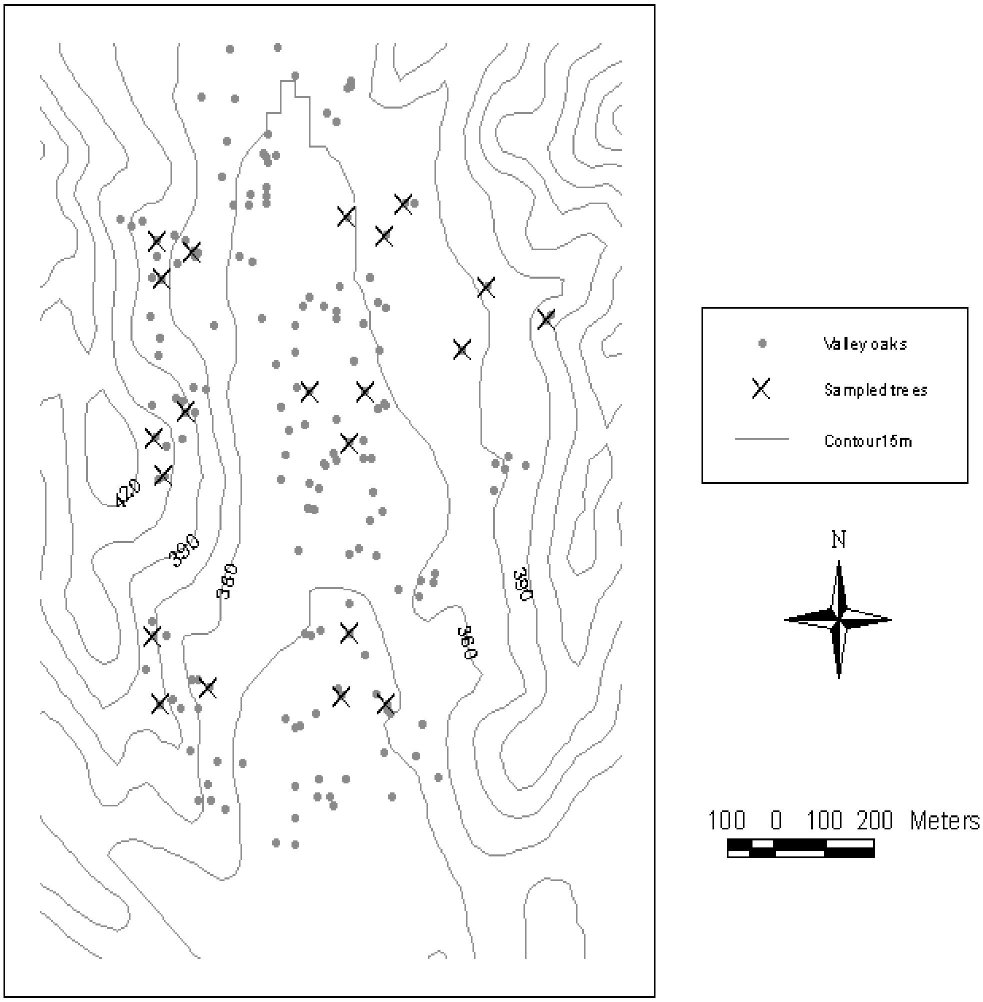

Figure 1—Map of all valley oak adults at study site in Sedgwick Reserve, Santa Barbara Co., California.

Valley oak density for the study site and for neighborhoods surrounding individual trees were estimated using mapped tree locations. ArcInfo™ (ESRI, Inc). A loose minimum bounding rectangle around 153 mapped valley oaks encompassed roughly 128 hectares, yielding a stand density of 1.19 trees/ha. Second order analysis of K-function statistics (Getis and Franklin 1987) indicates that trees are significantly clustered in the study area at all spatial scales. Thus, if a tree's neighborhood is defined as a circle of radius 150 m, roughly 3 standard deviations in our Gaussian pollen dispersal model (Sork and others 2002), centered on the tree canopy, the average neighborhood density for the 21 study trees is $\overline{D}$ = 1.62 trees/ha. The local neighborhood density, however, varies considerably for the 21 focal trees, ranging from D = 0.14 - 3.54 trees/ha (*table 1*). If we view local density as a signal of environmental effects that might affect seed traits, these raw stem counts are appropriate measures.

Table 1—*Local and weighted densities of conspecific adults surrounding each study tree, number of acorns sampled, mean proportion germinated, and mean acorn weight of 21 valley oak study trees collected in fall 1999 at Figueroa Creek, Sedgwick Reserve, Santa Barbara County, California.*

Study tree	Local density (*D*)	Weighted density (Δ)	Number sampled	Proportion germinated	Acorn weight (g)
1	0.57	1.39	70	0.600	8.66
2	0.99	1.26	83	0.518	5.24
3	0.71	0.41	6	0.674	8.50
4	0.42	0.10	51	0.118	8.29
5	0.28	1.00	7	0.572	5.93
6	0.14	0.05	108	0.334	8.57
7	1.84	2.59	59	0.187	6.98
8	2.12	6.12	21	0.248	7.47
9	2.55	3.21	12	0.083	5.76
10	1.27	2.50	19	0.421	4.97
11	1.56	3.24	75	0.147	6.73
12	1.27	3.10	24	0.125	4.06
13	1.84	5.52	14	0.357	8.23
14	1.27	2.47	76	0.132	5.99
15	1.56	3.59	27	0.185	9.97
16	1.84	5.66	38	0.316	7.22
17	2.55	5.73	12	0.000	9.09
18	2.26	4.68	63	0.571	5.96
19	2.83	3.31	27	0.556	4.88
20	2.41	3.88	142	0.908	6.94
21	3.54	6.50	61	0.082	6.74

The blue oak findings (Knapp and others 2001) imply that density is more appropriately viewed as a statement about pollen availability. To account for the steep exponential drop in probability of pollination with tree separation distance (Sork and others 2002), we also calculated a local neighborhood density, in which a neighboring tree's contribution to local density (Δ) was scaled by its distance (δ_i) to the focal tree, using the formula:

$$(\delta_i) = \exp\{-\,0.0002 * d_i^2\},$$

and

$$\Delta = \Sigma_i\ \delta_{i,} \text{ for all trees within 150 m of the focal mother,}$$

where the exponential coefficient (0.0002) is $(2\sigma^2)^{-1}$ (see Austerlitz and Smouse 2001, 2002), with σ^2 estimated as 2,500 m^2 (Sork and others 2002). These weighted local densities also vary among the 21 focal mother trees (*table 1*). The average value is 3.15, but the values ranged over two orders of magnitude, from 0.05 - 6.50.

Collection and Greenhouse Work

We visited the site repeatedly, from October through mid-November 1999, to collect mature acorns, up to 100 acorns for some trees. Individual trees in the study area were mapped using a 1993 digital panchromatic orthophoto with 1 m^2 resolution, produced by the U.S. Geological Survey (U.S. Department of the Interior 1992). Acorns were shipped to the Sork lab in St. Louis, where they were weighed individually and then planted into 12 in. deep pots. We planted acorns 1 cm below the soil (Pro-Mix BX), with six to nine acorns from the same family together in one or more pots, depending on family size. We watered acorns as needed and kept them under a 12 hr light regime. We monitored the pots weekly until radicals began to emerge from the soil, and then we monitored every 2-4 days. We marked newly emerging seedlings individually and recorded their dates of emergence. We defined successful germination as emergence of an above ground radical within 90 days of planting. For each maternal plant, we calculated the percentage of germination as the number of acorns germinated, out of the total number of seed planted for that tree.

Laboratory Analysis

For the mating system study, our goal was to assay 20 seedling genotypes for each of the 21 focal trees, but some trees yielded low germination rates. Realized sample sizes for the mating system study ranged from 4-20 progeny per focal tree, with only 19 of the 21 focal trees represented. We used a combination of ten allozyme and one microsatellite loci as the genetic markers for this study, a strategy deployed because the allozyme loci provided expeditious and inexpensive genetic screening, and the microsatellite locus provided valuable genetic resolution (Smouse and others 2001). Details of our methods of identifying the allozyme and microsatellite loci are given elsewhere (for enzymes also see Gram and Sork 2001, Sork and others 1997, Sork and others 2002). Allozyme loci are: *fluorescent esterase* (*Fe*, EC 3.1.1.1,), *leucine aminopeptidase* (*Lap*, EC 3.4.11.1), *phosphoglucose isomerase* (*Pgi*, EC 5.3.1.9), *malate dehydrogenase* (*Mdh*, EC 1.1.1.40), *phosphoglucomutase* (*Pgm*, EC 2.7.5.1), *menadione reductase* (*Mnr*, EC 1.6.99.-), and *triosephosphate isomerase* (*Tpi*, EC 5.3.1.1). The microsatellite primer was QpZAG110, originally developed for *Quercus petrea* (Steinkellner and others 1997).

Data Analysis

Ritland's MLTR program (Ritland 1990) generates three mating system parameter estimates that we focus on in this paper: (a) the outcrossing rate (estimated from multilocus genotypes, t_m, and from the average single-locus estimate, t_m); (b) the probability of mating among relatives (t_m - t_s); and (c) the probability of mating among full-sib relatives (the likelihood that two randomly selected offspring from a single mother share the same father, r_p), which can be translated into an estimate of effective number of pollen donors (N_{ep}= $1/r_p$). MLTR uses maximum likelihood analysis to provide minimal variance estimates of these parameters under a mixed mating model that assumes that a portion of the matings represent selfing and that the remaining portion are due to random non-self mating. We conducted MLTR with an EM algorithm, using 1,000 bootstrap replicates for the estimation of confidence intervals.

We were forced to pool microsatellite alleles into eight categories, due to the limitations of MLTR. We pooled the rare alleles by grouping them into three 'allelic classes', taking care that the new 'allelic classes' did not alter the probability of a mother producing a selfed offspring (e.g., we ensured that rare alleles were not pooled into alleles that were present in the maternal genotype). MLTR was run with two different parameter specifications: (1) We estimated the adult inbreeding coefficient (F) simultaneously with the other mating system parameters. (2) We fixed the adult F-value at zero. We use both strategies for adult inbreeding (F), because we do not know the inbreeding structure of the adults *a priori*, and these two estimates provide upper and lower bound estimates for the other mating system parameters.

To determine whether seed weight, transformed as $\log_e$(seed weight), differed between mothers, we conducted a one-way Kruskal-Wallace test (Proc NONPAR1WAY, SAS version 8). For the germination data, we analyzed the number of germinated and non-germinated seeds for each mother by way of a 21 x 2 contingency table (Conover 1999).

We examined the spatial patterns of average $\log_e$(seed weight) and percent germination (arc sine square root transformed) for the 21 maternal plants, using Canonical Correspondence analysis (Proc CANCORR, SAS version 8). The dependent (response) variables are mean seed weight and percent germination per maternal tree. The independent (predictor) variables were the X and Y spatial coordinates of each tree. Because the model includes precisely two response and two predictor variables, only two canonical axes result, only the first of which turns out to be useful. We also conducted the canonical correspondence analysis using local density and weighted local density values for each maternal tree to see whether these variables improved the model or were more important than the spatial variables.

Results

Mating System Analysis

The number of alleles per locus varied from 2-17. Recall that the 17 microsatellite allele frequencies were pooled into 8 allelic classes because the MLTR program can only handle 8 alleles (for raw allele frequencies at all 11 loci, see Sork and others 2002). The exclusion probability associated with this collection of loci is 92 percent, so genetic resolution of the assay battery is high (Sork and others 2002).

We estimate the multilocus outcrossing rate (t_m) for valley oak to be 96 percent, indicating some degree of selfing (*table 2*). Simultaneous estimation of t_m, t_s, and F in the mixed mating model yields a significant estimate for inbreeding in the adul$_{ts}$ (F = 0.243). The estimates of the single locus outcrossing rate (t_s), which include both self-mating and mating with relatives, were both ~ 0.96, the same as the multilocus estimate (t_m), regardless of whether F for the adult population was set to $F = 0$ or was allowed to float ($F = 0.243$). Thus, the resulting estimate of the portion of consanguineous mating was 0.00. The range of estimates of effective number of pollen donors, $N_{ep} = 1/r_p$, was 4.7-7.1 individuals, depending on whether we use $F = 0$ or $F = 0.243$. Either way, N_{ep} is the same order of magnitude we had estimated earlier, using TwoGener methods (Sork and others 2002).

Table 2—*Mating system parameters for valley oak population at Sedgwick Reserve, Santa Barbara Co. based on two versions of the MLTR model:* F *fixed at 0 and* F *was jointly estimated (Floating* F*) by seeding the program with* F *= 0.10.*

Mating system parameters	**Fixed *F***	**Floating *F***
Parental F estimate (SD)	0.000 (set)	0.243 (0.081)
Multilocus t estimate (SD)	0.957 (0.020)	0.957 (0.020)
Single locus t estimate (SD)	0.956 (0.011)	0.957 (0.012)
Consanguineous matings, t_m-t_s (SD)	0.001 (0.012)	-0.001 (0.011)
Correlation of t estimate, r_s (SD)	0.048 (0.014)	0.046 (0.013)
Correlation of p estimate, r_p (SD)	0.214 (0045)	0.141 (0.033)
Effective number of donors, N_{ep}	4.7	7.1

Germination and Seed Weight

Germination ranged from 0 – 91 percent (*table 1*) and was significantly different among mother trees (Contingency Table, df = 20, $\chi^2 = 334.9$, $P << 0.001$). Average acorn weight, varied from 4-10 grams (*table 1*) and differed significantly among mother trees (Kruskal-Wallis test, $\chi^2 = 365.77$, df = 20, $P = 0.0001$).

This variation in germination and acorn weight is not distributed randomly throughout the study area. The canonical correspondence analysis indicated a linear spatial trend in bivariate combination of mean percent germination and seed weight (*table 3*). The adjusted canonical correlation for the first canonical axis is 0.58, relatively high but not quite significant for the degrees of freedom in our model (*table 3*, $p = 0.066$, df = 4, 34). As summarized by the first canonical axis, the study site has an underlying spatial gradient with smaller acorns and lower germination success in the southwest corner and larger acorns and higher germination in the northeast corner (*fig. 2*). This trend does not correspond to elevation patterns shown in *figure 1*. Soils vary somewhat across the site, ranging from silty clay soils developed on Pleistocene colluvium to silty clay loams derived from recent alluvial deposits. However, this variation occurs along an east-west rather than north-south axis, and there is no apparent relationship between fruit characteristics and soil. With the exception of the trees at the south end of the plot, trees within clusters showed similar reproductive phenotypes (*fig. 2*). We also conducted a canonical correspondence model that included the density variables, but the results were not significant and are not presented. At this time, we have no additional genetic or environmental variables to associate with this nonrandom distribution of acorn traits.

Table 3—*Summary of results of canonical analysis of germination percentage (arc sine square root transformed) and seed weight (log$_e$ transformed) versus the spatial X- and Y-coordinates of 21 study trees.*

Parameter	Canonical axis 1	Canonical axis 2
Canonical correlation	0.626	0.078
Adjusted correlation	0.586	----
Eigenvalue	0.644	0.006
Likelihood ratio	0.605	0.994
F-test	2.430	0.110
Numerator df	4	1
Denominator df	34	18
Probability > F	0.066	0.745

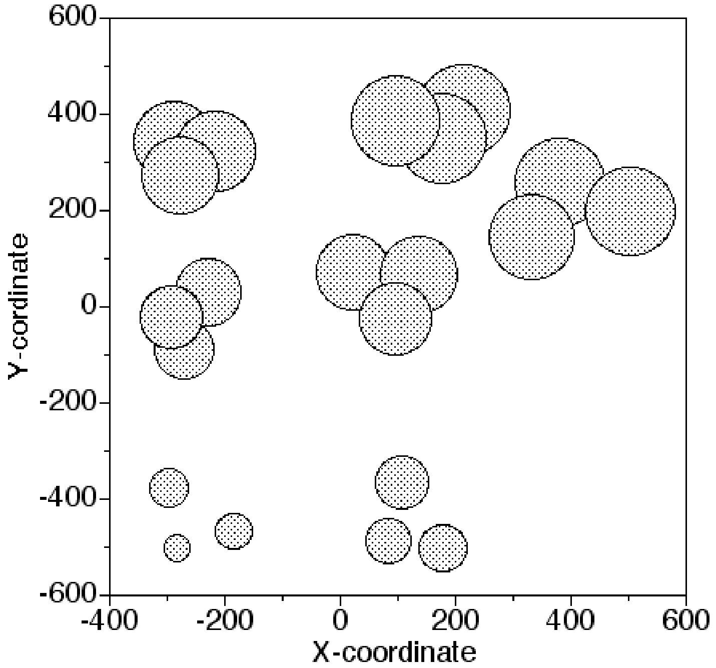

Figure 2—Map of the spatial pattern of the first canonical axis (CA 1) of multivariate combination of germination and mean acorn weight per study tree. Bubble size is positively associated with percent germination and acorn size. (See *table 4* for correlation of reproductive variables with CA 1.)

Our 1999 data do not reveal a strong correlation between germination percentage and mean seed weight (*r* = - 0.09; *table 4*), but we do find that both germination and seed weight are positively associated with the North/South axis (Y) and the bivariate W1 axis, which is correlated more strongly with Y-axis (*r* = 0.96) than the X-axis (*r* = 0.51). The first canonical axis, W1, is loaded almost evenly by mean seed weight and germination percentage (*r*= 0.44, 0.41, respectively, *table 4*). The correlations of local and weighted local density with germination were negative but not significant (*r* =-0.25, -0.29, p =0.28, 0.20, respectively). The correlations with seed weight were also not significant (*r* = -0.17, 0.02, *p* = 0.46, 0.92, respectively).

Table 4—*Correlations among reproductive and spatial variables associated with 21 study trees. Germination percent and acorn weight were transformed as described in text. W1 and W2 are the canonical axes for the reproductive variables. V1 and V2 are the first two canonical variables associated with the X- and Y-coordinate. Correlations are above the diagonal and significance values are below.*

	Germ	Weight	X	Y	W_1	W_2	V_1	V_2
Germ	**1.000**	-0.086	0.271	0.402	0.438	0.055	0.700	0.714
Weight	0.711	**1.000**	0.157	0.407	0.408	-0.059	0.651	-0.759
X	0.234	0.496	**1.000**	0.236	0.511	0.860	0.320	0.067
Y	0.070	0.067	0.304	**1.000**	0.956	-0.294	0.598	-0.023
W_1	0.047	0.067	0.018	0.000	**1.000**	0.000	0.626	0.000
W_2	0.811	0.800	0.000	0.196	1.000	**1.000**	0.000	0.078
V_1	0.000	0.001	0.158	0.004	0.002	1.000	**1.000**	0.000
V_2	0.000	0.000	0.774	0.922	1.000	0.738	1.000	**1.000**

Discussion

Mating System

The population of valley oak at Sedgwick Reserve has a very high outcrossing rate (96 percent) but no apparent mating among relatives ($t_m - t_s = 0$). The high outcrossing rate is expected for wind-pollinated trees species and has been observed for other oak species (e.g., t_m = 100 percent for *Quercus rubra* (Schwarzmann and Gerhold 1991) and *Q. alba*[6] and *Q. velutina* (Fernandez and others 2002). Given our previous finding that average pollen movement is ~ 65 m (Smouse and others 2001), the lack of mating among relatives is a bit unexpected, but such a result may indicate that neighbors at our study site are not closely related. We have preliminary evidence showing a lack of significant autocorrelation among adults,[6] which is consistent with that interpretation, but it is based on the 21 study trees only. In sum, the mating system we examined during the 1999 field season indicates a population with no mating among relatives but some degree of selfing.

This study supports our earlier finding that valley oak has relatively few effective pollen donors (Sork and others 2002); we estimated N_{ep} = 4.7-7.1 'effective fathers' for $F = 0$ and $F = 0.243$, respectively. We have far too few adults to estimate the parental inbreeding coefficient with any precision (the confidence interval extends from $0.0 \leq F \leq 0.60$), and it is difficult to say anything definitive about F under those conditions. The lower value here is compatible with the range of N_{ep} estimates (3 - 5) obtained from our TwoGener analysis, but the larger point is that all of these estimates indicate very few effective pollen donors. Pollen can move long distances in this savanna setting, and there are probably long distance pollination events contributing to the genetic variation we encounter in the seedlings of these focal mothers, but they represent minor contributors to the total seedling pool; most pollination is exceedingly local. Our *Quercus lobata* values are at the lower end of the range of values reported for other studies that use MLTR to estimate N_{ep}. For example, Western larch (*Larix laricina*) has ~35 effective pollen donors (El-Kassaby and Jaquish 1996), *Pinus washoensis* has ~14 effective donors (Mitton and others 1997) and *Grevillea iaspicula*, an endangered shrub in the Proteaceae, has 2 - 3 effective pollen donors (Hoebe and Young 2001). In Missouri Ozark forest with high tree density, our TwoGener estimate of N_{ep} indicated that *Quercus alba* had ~ 8 effective pollen donors (Smouse and others 2001). Based on an MLTR analysis, *Quercus velutina* in a closed Ozark forest had ~6 effective donors. Thus, the low number of effective donors that we have observed in valley oak indicates that, in spite of the open landscape conditions that should permit pollen to move more freely across the landscape (Okuba and Levin 1989), most pollination is very localized.

We will comment briefly on the differences in estimates generated by MLTR and TwoGener. The mixed mating model uses a maximum likelihood approach to jointly estimate a selfing rate and the effective outcrossing rate assuming random mating throughout the population. If the scale of population exceeds the scale of pollen movement, the assumption of random mating throughout the area is violated. On the other hand, TwoGener makes no assumption about random mating but it does assume no inbreeding in the parental population. If F is large, then TwoGener underestimates the effective number of pollen donors, but we can adjust that estimate for $F > 0$ (Austerlitz and Smouse 2002). If $F = 0.243$, the adjusted TwoGener

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[6] Unpublished data on file at the web address: http://mofep.conservation.state.mo.us (this information is only available with permission from VLS).

estimate of $N_{ep} = 4.57$, still somewhat smaller than the corresponding estimate from MLTR, which is $N_{ep} = 7.1$. For conservation, restoration and management purposes, both estimates are telling us that contemporary pollen flow is spatially restricted, severely so.

Variation in Recruitment-relevant Seed Traits

We found a great deal of heterogeneity across study trees in germination and seed weight. As poorly estimated as *F* is, from this limited sample size, we are hesitant to suggest that inbreeding depression is contributing to that heterogeneity. With greater sample size per tree in future studies, we will be able to test the association between the selfing and biparental inbreeding rates with seed traits. We will also test whether localized density affects those traits once we have a larger sample size of trees and a greater variance in density. At this point, we cannot conclude whether the trend is confined to this set of trees or is a reflection of some larger gradient within Sedgwick Reserve. To determine whether the gradient in seed trait*s* reflect environmental effects alone or whether the adult population has an underlying genetic structure, we are expanding the study area and increasing the sample size of focal mother trees, which should permit a more definitive analysis of the genetic structure of the adult population.

Implications for Management of Valley Oak

Our results indicate that this population of valley oak is highly outcrossing but may have limited pollen movement. Given the ongoing loss of valley oak stands in the region, additional research is needed to assess the relationship between local tree distribution pattern and reproductive isolation (and associated reduction in acorn crop size). Such information could help ongoing oak conservation and restoration efforts in the region to evaluate impacts of additional stand fragmentation and could also guide patterns of restoration plantings. Our ongoing research at Sedgwick Reserve, expanded to study pollen flow and fruit production for a much larger sample of trees over the next several years, is designed to contribute such information.

Acknowledgments

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The Potential Impacts of Development on Wildlands in El Dorado County, California[1]

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Abstract

We modeled future development in rapidly urbanizing El Dorado County, California, to assess ecological impacts of expanding urbanization and effectiveness of standard policy mitigation efforts. Using raster land cover data and county parcel data, we constructed a footprint of current development and simulated future development using a modified stochastic flood-fill algorithm. We modeled combinations of constraints from the 1996 County General Plan and parcel data—slope, stream buffers, oak canopy retention, existing development, public ownership, regional clustering, and acquisition programs—and overlaid development outcomes onto the land cover data. We then calculated metrics of habitat loss and fragmentation for natural land cover types. Rural residential development erodes habitat quality much more than habitat extent. Policy alternatives ranging from existing prescriptions to very restrictive regulations had marginal impact on mitigating habitat loss and fragmentation. Historic land parcelization limits mitigation of impacts by the current General Plan prescriptions that only apply when a parcel requires subdivision before development. County-wide ordinances were somewhat more effective in preserving habitat and connectivity. These solutions may not offer enough extra protection of natural resources to justify the expenditures of "political capital" required for implementation. Custom, parcel based acquisition scenarios minimized habitat loss and maximized connectivity. Better analysis of public policy and planning design may be a more effective "smart growth" tool than generic policy prescriptions.

Introduction

The California Department of Finance projects the State's population to increase from 34 million to over 45 million by the year 2020 (California Department of Finance 2001). During the past 20 years, the spatial distribution of California's population has also changed as more people moved to the periphery of the dense Los Angeles and San Francisco Bay metropolitan areas and to the historically lower density Central Valley and Sierra Nevada foothills (U.S. Census Bureau 1991, 2001). Since the eastern half of many of these Sierran counties is predominantly national forest above 1,500 meters, the vast majority of this additional population will reside in the lower elevation foothills, a region dominated by oak hardwood savannah. The hardwood rangeland region of the Sierra, extending from 100 to 1,500 meters in elevation, is almost exclusively privately owned and has historically been used for grazing and some dryland farming (Duane 1996, Greenwood and others 1993). The switch from large parcel, low to moderate intensity agriculture to small parcel, high intensity urban and ex-urban land use promises great change to the natural

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ecosystems of the foothills region. These 5-acre to 40-acre ranchettes will likely contain the majority of naturally functioning hardwood landscape in the near future.

One such region of rapid change is El Dorado County in the Central Sierra Nevada Mountains. We conducted a policy analysis of the El Dorado County General Plan by modeling development in the western, foothill portion of the county. We were interested in two topics: 1) ecological impacts on wildland habitat resulting from expanding urbanization under the County's General Plan; and 2) the effectiveness of commonly proposed land use policy initiatives to mitigate those impacts. Several models exist for projecting development expansion at the county and regional scale (Landis 1994, 1995, 1998a, 1998b; Johnston 2000, 2001; US Environmental Protection Agency 2000). These models focus on dense urban development (1 - 2 acre parcels or smaller) using economic formulas of land values and empirically derived “attractors” of development such as proximity to existing infrastructure (roads, sewer, water, etc.) to guide development probabilistically and incrementally over time. However, in rural areas (5 - 40 acre parcels), where attractors are less obvious or more difficult to model, or where tractable economic factors are not the primary drivers behind development decisions, these models generally ignore rural development or resort to random allocation (Johnston 2001). In El Dorado County, the General Plan designates 23 percent of the county for development in this rural density range. In order to adequately predict impacts in these regions, we needed to place the existing and potential footprint of development as explicitly as possible. We developed a cell-based, empirical model that characterizes development patterns from existing development and then extends those patterns across the landscape onto vacant lands. Because we were primarily concerned with the relative impacts of the county's General Plan and alternative policy proposals, we chose to extend development to full “buildout” of the General Plan, approximately a 20-year time horizon, rather than incorporating an economic component which might allow the phasing of development over time.

We began by determining where development existed in 1996, the most recent year for which digital parcel data were available. We then predicted where development would be at full buildout of the General Plan under various scenarios (e.g., uncontrolled vs. smart growth, strict vs. loose environmental land use policy, and combinations thereof). For any given scenario, our model can assess the implications for a variety of issues ranging from natural ecosystem functions to local and regional economies to general quality of life. At present, we have analyzed a wide range of land use policies in the County and their relative impacts on two major areas of concern, wildland habitat quality (characterized by extent, fragmentation, and configuration) and economic costs and losses due to wildfire. This paper presents our research on the former.

Study Area

El Dorado County is a predominantly rural county in the Central Sierra region of California stretching from the floor of the Central Valley east of Sacramento to the crest of the Sierras and the southern portion of Lake Tahoe (mean latitude 38.75° N, mean longitude 120.5° W). The county's 463,500 hectares cover a wide diversity of habitats including low elevation annual grasslands and blue oak (*Quercus douglasii*) savannah at the western edge, mid-elevation oak woodlands and mixed oak-conifer-shrub complexes in the central region, and Sierran mixed conifer forest dominated by

Figure 1—Location of study area with major highways and cities.

ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*Pinus jeffreyi*), and lodgepole pine (*Pinus contorta*) in the eastern half. According to the 2000 Census (U.S. Census Bureau 2001), 156,299 people lived in El Dorado County at an overall density of 33.7 persons/km^2. However, because the eastern half of the county is almost entirely national forest except for settlements on the southern littoral edge of Lake Tahoe, the average density for private lands is 63.3 persons/km^2. Housing density is 28.9 units/km^2. Our study area encompasses 220,954 ha and is restricted to the predominantly privately owned western foothills region of the county (*fig. 1*).

From the time Gold Rush pioneers settled in the 1850s, the population of El Dorado County fluctuated between 6,000 and 20,000 people until the 1950s. Since that time the decadal growth rate has ranged from 20 percent to 100 percent, with growth rates of 46.8 percent and 24.0 percent in the 1980s and 1990s, respectively (U.S. Census Bureau 1991, 2001). State Department of Finance projections indicate this magnitude of growth continuing for the next two decades resulting in 252,900 residents by 2020 (California Department of Finance 2001).

Methods

Study Design

The purpose of this study was to evaluate the potential impact of El Dorado County's General Plan on wildland habitat in the county (primarily oak woodland) and how policy alternatives might mitigate these impacts. We modeled several alternative scenarios, three iterations each, by varying one or more of the General Plan prescriptions, as well as the possible spatial configuration of future development (*table 1*), and overlaying the resulting footprint of development onto the land cover data and measuring the core extent, fragmentation and configuration of wildland. As we intended this work to be directly relevant to issues facing the county, many of these scenarios were devised from suggestions by residents and county officials. Thus, we did not attempt to analyze every possible combination of variables, especially as it became apparent that one of them was not proving to be effective in mitigating the impacts on wildland.

We used three main geographic information system (GIS) datasets as inputs: 1) 1990 Hardwood Rangelands Pixel Data (Pacific Meridian Resources 1994) for land cover and current footprint of development (*fig. 2a*); 2) 1996 County Assessor's parcel data for land tenure information; and 3) 1996 Adopted County General Plan for future potential development densities (*fig. 2b*). We converted the parcel and General Plan data to 25 m raster grids and snapped them to the Hardwoods data. We conducted all spatial modeling with ESRI's ARC/INFO and GRID software (vers. 7.1.1 - 8.1) on UNIX workstations except the fragmentation metrics, which we calculated using APACK v. 2.15 (Mladenoff and DeZonia 2000) on a Windows2000 operating system. An in-depth detail of our methodology has been previously published on the CDF-FRAP website (Greenwood and Saving 1999). Here, we present only a basic overview.

Creating the Footprint of Development

In order to model future development, we first had to construct a pixel-based *footprint of current development* which showed as explicitly as possible where structures and other human disturbances to the natural landscape exist. Remote sensing-based pixel data, such as the Hardwoods data, serve this purpose to some degree, especially in rural areas (Merenlender and others 1998, Ridd and Liu 1998), but provide no context of land use. Such data also miss development obscured by tree canopy and tend to confuse some urban and non-urban land cover types (e.g., rock outcrops and concrete) (Bruzzone and others 1997, Fisher and Pathirana 1990, Quarmby and Cushnie 1989). From the parcel data we determined the land use of each parcel and thus derived two binary layers—development status (*developed* or *vacant*) and intensity of use (*intense* or *not intense*) at the parcel level. For *developed* and *intense* parcels smaller than 1 hectare (2.5 acres), we included the entire parcel in the footprint. However, for larger parcels we turned to the Hardwoods data to identify specific areas of human disturbance within the parcel. We compared the classes Urban and Other (U/O) from the Hardwoods data to the development status of the parcel data. Where a U/O pixel(s) existed inside a *developed* parcel, we included those U/O pixels in the *footprint of current development*. Where a U/O pixel(s) existed in a *vacant* parcel, we considered those pixels "false positives" and did not include them in the *footprint of current development*, although they did remain in the land cover layer as Barren. For *developed* parcels with no U/O pixel(s), we simulated a pattern of development in the parcel using the same technique to project future development patterns (see below). Thus, we created a picture of current development composed of three elements: 1) small, intensely used parcels; 2) scattered pixels of development in larger parcels; and 3) stochastically placed pixels in developed parcels within which we could not determine the explicit location of development (*fig. 2c*).

Table 1—*Descriptions of the combinations of restrictions used for each scenario tested.*

	Slope/Stream Restrictions			Canopy Retention[1]			Other Restrictions			Total Area (ha)
Scenario	**Description**	**Extent**	**Area (ha)**	**Description**	**Extent**	**Area (ha)**	**Description**	**Extent**	**Area (ha)**	**Restricted[6]**
500	Present Condition	-	-	-	-	-	-	-	-	-
503	25 m stream setbacks, < 40% slope	subdiv.	19,567	as per GP	subdiv.	5,980	-	-	-	122,774
504	25 m stream setbacks, < 40% slope	all	26,983	as per GP	subdiv.	5,980	-	-	-	128,389
505	50 m stream setbacks, < 40% slope	subdiv.	23,319	as per GP	subdiv.	5,980	-	-	-	125,988
506	50 m stream setbacks, < 40% slope	all	31,819	as per GP	subdiv.	5,980	-	-	-	132,694
507	25 m stream setbacks, < 40% slope	subdiv.	19,567	as per GP	subdiv.	5,980	Clustering[3]	LDR, subdiv.	12,526	122,774
508	25 m stream setbacks, < 40% slope	subdiv.	19,567	as per GP	subdiv.	5,980	Clustering[4]	LDR, subdiv.	12,526	122,774
509	25 m stream setbacks, < 40% slope	subdiv.	19,567	Increased[2]	subdiv.	7,096	-	-	-	123,920
513	25 m stream setbacks, < 40% slope	subdiv.	19,567	as per GP	all	6,409	-	-	-	123,368
514	25 m stream setbacks, < 40% slope	all	26,983	as per GP	all	6,409	-	-	-	128,944
515	50 m stream setbacks, < 40% slope	subdiv.	23,319	as per GP	all	6,409	-	-	-	126,564
516	50 m stream setbacks, < 40% slope	all	31,819	as per GP	all	6,409	-	-	-	133,217
520	50 m stream setbacks, < 40% slope	all	31,819	as per GP	all	6,409	Clustering[4]	LDR, subdiv	12,526	133,127
543	25 m stream setbacks, < 40% slope	subdiv.	19,657	as per GP	subdiv.	5,980	Acquistion[5]	AOC	2,071	124,513

[1] Canopy retention restricts development by limiting the amount of development. In most cases, this does not mean complete restriction but rather a reduction in density only (*table 2*). See Greenwood and Saving, 1999.

[2] For details, see Greenwood and Saving, 1999.

[3] Proportion (B) of developed cells increased from 9% to 14%. Adjacency (C) increased from 55% to 95%.

[4] Proportion (B) of developed cells increased from 9% to 14%. Adjacency (C) increased from 55% to 98%.

[5] We manually selected parcels to be restricted from development in Areas of Concern (AOC).

[6] Includes all restrictions plus existing *developed* parcels, parcels *closed to development*, public ownership, and areas designated Open Space (OS) in the General Plan.

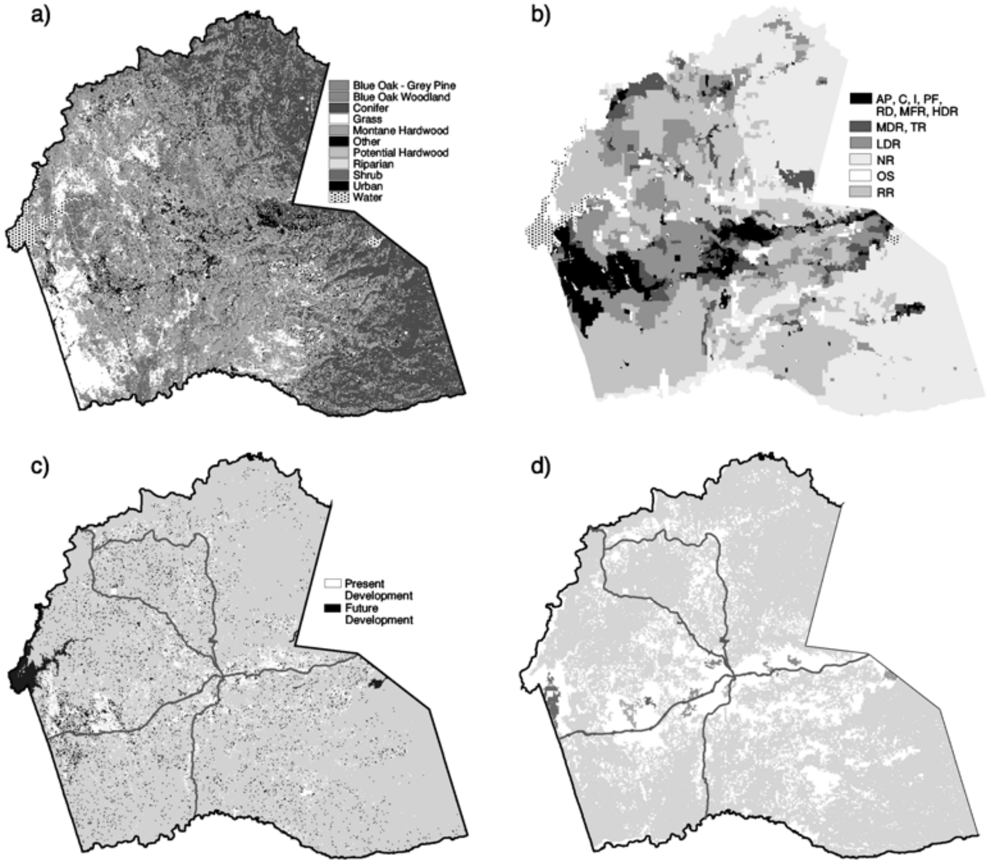

Figure 2—a) Land cover types from 1990 Hardwoods Pixel Data (Pacific Meridian Resources 1994), b) 1996 El Dorado County Adopted General Plan land use classes collapsed to 6 categories (see *table 2* for land use codes), c) footprint of current and future development under General Plan scenario (503), and d) map of current wildland habitat in the study area.

The first step in creating the *footprint of future development* required knowing where development could *not* occur. From the General Plan we derived a restriction status for each parcel. A parcel was *closed to future development* if it were already developed and already at the minimum allowable lot size for that General Plan density class. Alternatively, a parcel was *open to development with restrictions* imposed by the General Plan (i.e., discretionary permit review) if it were *developed* or *vacant* but at least twice as large as the allowable minimum lot size, meaning the lot could be further subdivided. Finally, a parcel was *open to development without restriction* (i.e., ministerial review) if it were *vacant* and already at the minimum allowable lot size for that General Plan density class and therefore could not be subdivided further.

The General Plan contained three major restrictions applying to discretionary permit review that we were able to model spatially – 25 m (1 pixel) stream setbacks,[4]

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[4] The Adopted General Plan calls for 100' stream setbacks. Since our model is raster based, we used a one pixel (25 m) buffer as the closest estimate.

Table 2—*Canopy retention guidelines from Adopted General Plan. Values represent percentage of canopy that must be retained for each combination of General Plan Land Use Class and Current Oak Canopy Closure percentage. Where 100 percent of the canopy must be retained, no development can occur on oak pixels.*

	Current oak canopy closure (pct)				
General Plan land use class	**≤ 19**	**20-39**	**40-59**	**60-79**	**80-100**
Multi-family Residential (MFR)	90	85	80	70	60
High Density Residential (HDR)	100	90	80	70	65
Medium Density Residential (MDR)	100	90	80	70	65
Low Density Residential (LDR)	100	100	90	85	80
Rural Residential (RR)	100	100	100	95	90

no development on slopes over 40 percent, and an oak canopy retention guideline based on the density class of development and the existing canopy cover (*tables 1, 2*). We created a separate mask for each of these restrictions which could be turned on or off or, in order to simulate an ordinance, be applied to all parcels *open to development* regardless of restriction class. We also created similar masks reflecting 50 m stream buffers and increased canopy retention. Lastly, some areas were off limits to development in every scenario—areas classified as Urban or Other in the Hardwoods data, parcels that were *developed* and *closed to future development*, public lands, private reserves, easements, and open space designated in the General Plan.

Once we determined where development was allowable, we then determined the spatial configuration of development at the 25 m pixel scale. McKelvey and Crocker (1996) developed a stochastic flood-fill algorithm to create theoretical landscapes burned by fire using two aspects of spatial configuration—proportion (B) of landscape burned by fire, and the spatial adjacency (C) of the burned pixels. Adjacency is defined as the probability that if a cell is burned, an adjacent cell is also burned.[5] We modified their algorithm to create binary neutral landscapes that mimic the development patterns for each housing density class in the General Plan. By overlaying the Urban and Other pixels from the Hardwoods data onto classified 1990 Census block housing density data, we calculated proportion (B) and adjacency (C) for landscapes settled at different densities. The proportion of Urban and Other pixels ranged from 27 percent for housing density classes greater than 1 unit/acre down to 3 percent for density classes less than 1 unit/40 acres (*table 3*). Adjacency values varied to a lesser degree, ranging from 62 percent to 50 percent over the same housing density range (Greenwood and Saving 1999). By masking non-developable areas and inserting portions of these theoretical landscapes into the appropriate General Plan density region, we created potential *footprints of future development* for the study area (*fig. 2c*).

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[5] McKelvey and Crocker refer to the adjacency measure (C) as contagion. To avoid confusion with the contagion indices of O'Neill and others (1988) and Li and Reynolds (1993), we have chosen to use the term adjacency.

Table 3—*General Plan land use classes and allowable lot sizes with proportion of cells (B) from the Hardwoods data classified as Urban or Other and likelihood of adjacency (C) of Urban and/or Other cells.*

General Plan land use class	Allowable lot size (ac)	Proportion of urban or other cells (B)	Probability of adjacency (C)
Multi-family Residential (MFR), High Density Residential (HDR)[1]	<= 1	0.27	0.62
Medium Density Residential (MDR)[2]	1 - 5	0.14	0.61
Low Density Residential (LDR)	5 - 10	0.09	0.55
Rural Residential (RR)	10 - 40	0.06	0.55
Natural Resources (NR)	40 - 160	0.03	0.50

[1] Includes these General Plan Land Use Classes - Adopted Plan (AP), Commercial (C), Industrial (I), Public Facilities (PF), and Research and Development (RD)

[2] Includes Tourist Recreation (TR)

For most scenarios, we assumed the spatial configuration of development for a given density class would not be significantly different in the future than at present. In other words, the values of B and C for a given density class did not change. However, the model did not limit us to this assumption. The General Plan allows for the doubling of total housing density in the Low Density Residential (LDR) class (5 - 10 acre parcels) if the development is highly "clustered." Our landscape generator allowed us to easily simulate how this development pattern might appear (scenarios 507 and 508). We created two clustered density patterns for LDR by increasing B from 9 percent to 14 percent to simulate the density bonus, and by increasing C from 55 percent to 95 percent and 98 percent to simulate clustering (*table 1*).

Quantifying Impacts to Wildand Habitat

For this analysis, we defined *habitat* as all land cover types in the 1990 Hardwoods Pixel Data that were not Urban, Other, or Water. We combined Urban and Other pixels, along with developed cells from the *footprint of future development*, into one class called *developed*. Water was masked from the analysis environment. We defined *wildland habitat* as *habitat* more than 50 m (2 pixels) from a *developed* pixel, in patches greater than 100 hectares and containing no constrictions, or narrow necks, of *wildland habitat* narrower than 50 m. *Urban habitat* were those areas of natural vegetation within 50 m of a *developed* pixel. *Marginal habitat* were all areas not defined as *urban* or *wildland habitat* (narrow constrictions or patches less than 100 hectares, and > 50 m from *developed* pixels). This overlay of the footprint of development onto the natural land cover creates a landscape mosaic of *wildland*, *marginal* and *urban habitats*.

A quick review of the landscape ecology literature reveals many highly specialized metrics for capturing specific characteristics of a landscape. Several studies (Hargis and others 1999; McGarigal and McComb 1995, 1999; Ritters and others 1995; Tinker and others 1998) have shown that the simplest, most basic measures are the easiest to understand and serve well to compare and contrast landscapes. We calculated the following fragmentation metrics for wildland habitat for each scenario—total area, number of patches, mean patch size, largest patch size, mean shape index (Frohn 1998, McGarigal and Marks 1995, Ritters 1995), corrected mean perimeter/area (P/A) ratio (Baker and Cai 1992), and total edge density. Ritters (1995) inverts McGarigal and Marks' (1995) mean shape index for raster data, calling it "average normalized area, square model," to make the values range from 1.0 for a perfectly square patch to 0.0 for patches that are long and narrow. The APACK software calculates Ritters' metric. As this metric measures the same landscape attribute as McGarigal's mean shape index (shape complexity - patch shape relative to a square), we have chosen to use McGarigal's name, mean shape index, when referring to it rather than Ritters' more cumbersome moniker. Although these metrics provide an objective means of comparing landscapes, they do not quantify all aspects of landscape configuration. Therefore, we also assessed model results through visual inspection of the output maps of *wildland habitat* extent.

Results

General Plan

Figure 2d shows the present extent of *wildland habitat* in the study area. The dominant feature of the landscape is a single patch of wildland (mean area of three iterations, 159,535 ha) that extends across the county from north to south and bridges the Highway 50 corridor. The influence of development is substantial yet would appear not to have significantly disrupted the contiguity of wildlands outside of the Highway 50 corridor and the communities of Pilot Hill and Georgetown. *Figure 3a* shows how the county's wildlands might appear if the General Plan were completely built out (scenario 503). The most apparent impact is the increase in number of patches and the cleaving of the wildland into distinctly separate northern and southern regions. Compared to present conditions, mean number of patches per iteration double from 10.0 to 19.67 and mean patch size accordingly drops from 16,182 ha to 6,337 ha (*table 4*). Mean largest patch size similarly declines to 59,603 ha. As patch sizes drop, measures of total edge density and corrected perimeter-to-area (P/A) perforce increase. Mean total edge density rises from 46.6 m/ha to 68.4 m/ha while mean corrected patch P/A ratio increases from 8.97 to 9.76. Mean shape index decreases from 0.070 to 0.043 indicating that not only does wildland shrink and fragment, it also becomes more complex spatially due to low density development perforating the existing wildland matrix. It is important to note, however, that the significant loss of wildland does not mean that large portions of the county have been paved over. While the mean loss of wildland is 23 percent, only 4.5 percent of wildland is actually converted to urban use. For oak woodland land cover types, 40 percent of wildland becomes *marginal* or *urban* woodland but only 4 percent is physically lost to development. In other words, areas that once functioned under a more natural state and presumably provided functional habitat for species are degraded, either due to proximity to urban land uses or by isolation from larger patches of contiguous natural vegetation.

Table 4—*Mean values of wildland habitat landscape metrics for three iterations of the Present Condition (500) and General Plan (503) scenarios.*

	Present condition scenario 500	**General Plan scenario 503**
Total area	161,825 ha	123,267 ha
Number of patches	10.00	19.67
Mean patch size	16,182 ha	6,337 ha
Largest patch size	159,535 ha	59,603 ha
Mean shape index	0.070	0.043
Mean patch P/A ratio, corrected	8.974	9.762
Total edge density	46.57 m/ha	68.38 m/ha

General Plan Alternatives—Increased Development Restrictions

Figure 3 (*b-d* and *g-k*) shows extents of wildlands for the General Plan alternatives meant to mitigate impacts through increased restrictions to development. The most noticeable aspect of the maps is their similarity to the General Plan scenario. The north and south patches remain highly separated in all scenarios except for scenario 543 where a few small patches come close to reconnecting the north and south patches. The differences become more apparent when the metrics are examined. All scenarios maintain a greater area of wildland than the General Plan. Scenarios that increase the areal extent of development restrictions (504, 505, 506, 509, 513, 514, 515, 516) generally indicate a decrease in fragmentation (mean number of patches decreases slightly and mean patch size increases slightly) (*fig. 4*). However, the range for number of patches and mean patch size for these scenarios is high, indicating site-specific sensitivity to placement of development. Scenarios 506 and 516 show the greatest increase in wildland mean total area (126,716 ha and 126,877 ha, respectively) and mean largest patch size (60,906 ha and 61,105 ha, respectively). Scenarios 506, 509 and 516 have the highest mean patch sizes (6,805 ha, 7,021 ha, and 6,952 ha), although 509 has a large range (1,238 ha). These results are consistent with those expected as the scenarios 506 and 516 restrict the largest amounts of land from development (132,694 ha and 133,217 ha, respectively). Patch shape complexity shows little difference in all scenarios as mean shape index remains virtually unchanged as does the mean corrected patch P/A ratio. Mean total edge density declines slightly with 506 and 516 having the greatest decrease (67.02 m/ha and 67.00 m/ha, respectively).

General Plan Alternatives—Development Clustering

For scenarios 507 and 508 we examined the efficacy of clustering development for mitigating wildland habitat loss. For General Plan density classes of Low Density Residential (LDR), we increased adjacency (C) values to 95 percent and 98 percent, respectively. Because the General Plan allowed for a density bonus to the next higher density class, Medium Density Residential (MDR), we also increased the proportion (B) of developed pixels in LDR from 9 to 14 percent for both scenarios. Neither scenario shows a demonstrable increase in wildland habitat retention over the General Plan scenario, while some metrics indicate increased fragmentation. Mean

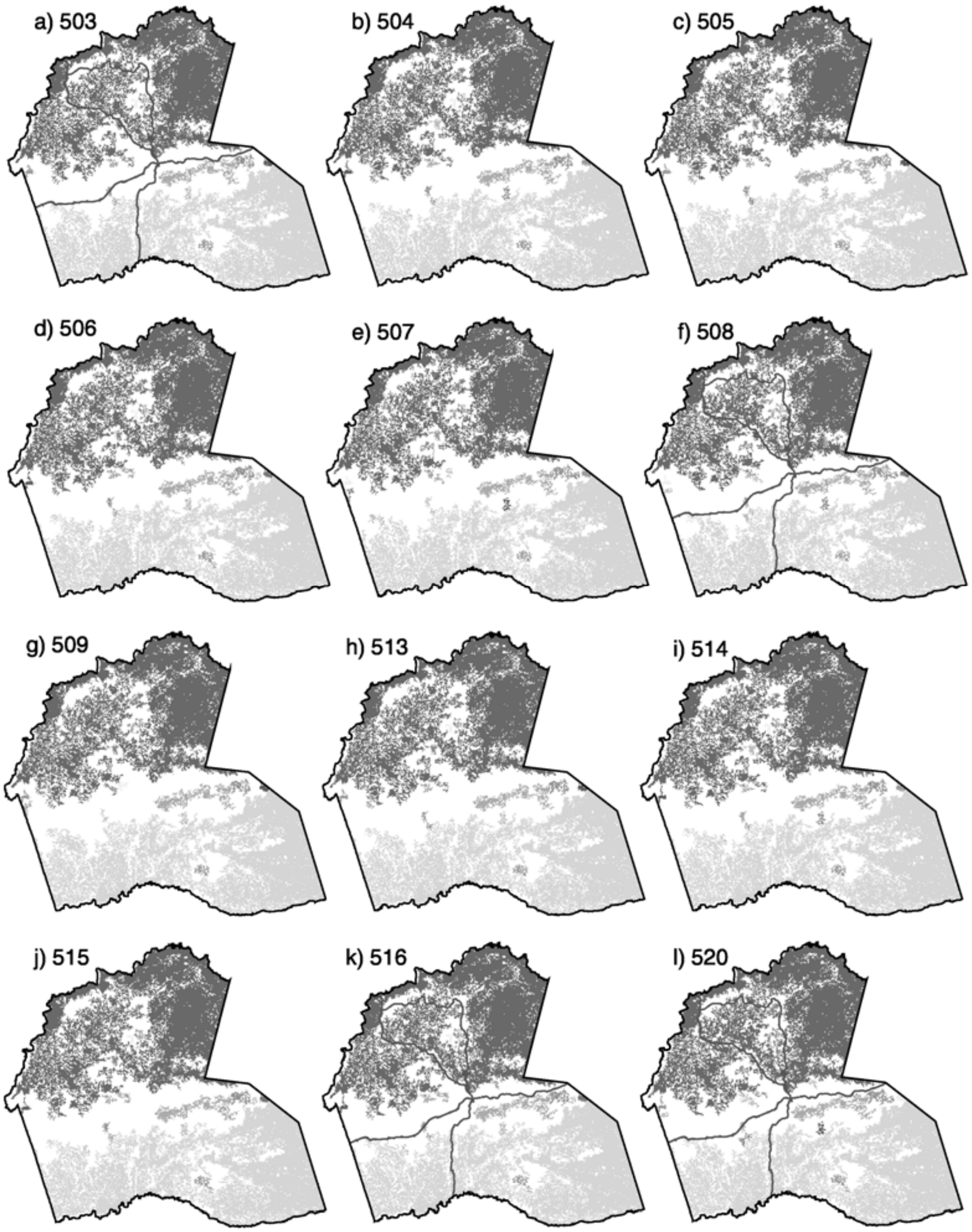

Figure 3—Maps of wildland habitat after full buildout for all scenarios. Areas of the same shade are a contiguous patch.

total area for scenario 507 (123,310 ha) is virtually the same as the General Plan and only slightly higher for scenario 508 (123,831 ha) (*fig. 4*). Mean largest patch size (507 = 59,502 ha, 508 = 59,847 ha) and mean corrected patch P/A ratio (507 = 0.044, 508 = 0.047) show similar behavior while mean total edge density does decrease slightly for 508 (67.39 m/ha). Mean number of patches (507 = 20.67, 508 = 19.0) remains within the range of values of those of the General Plan. Mean patch size actually goes down for 507 (5,979 ha) and remains unchanged for 508 (6,517 ha).

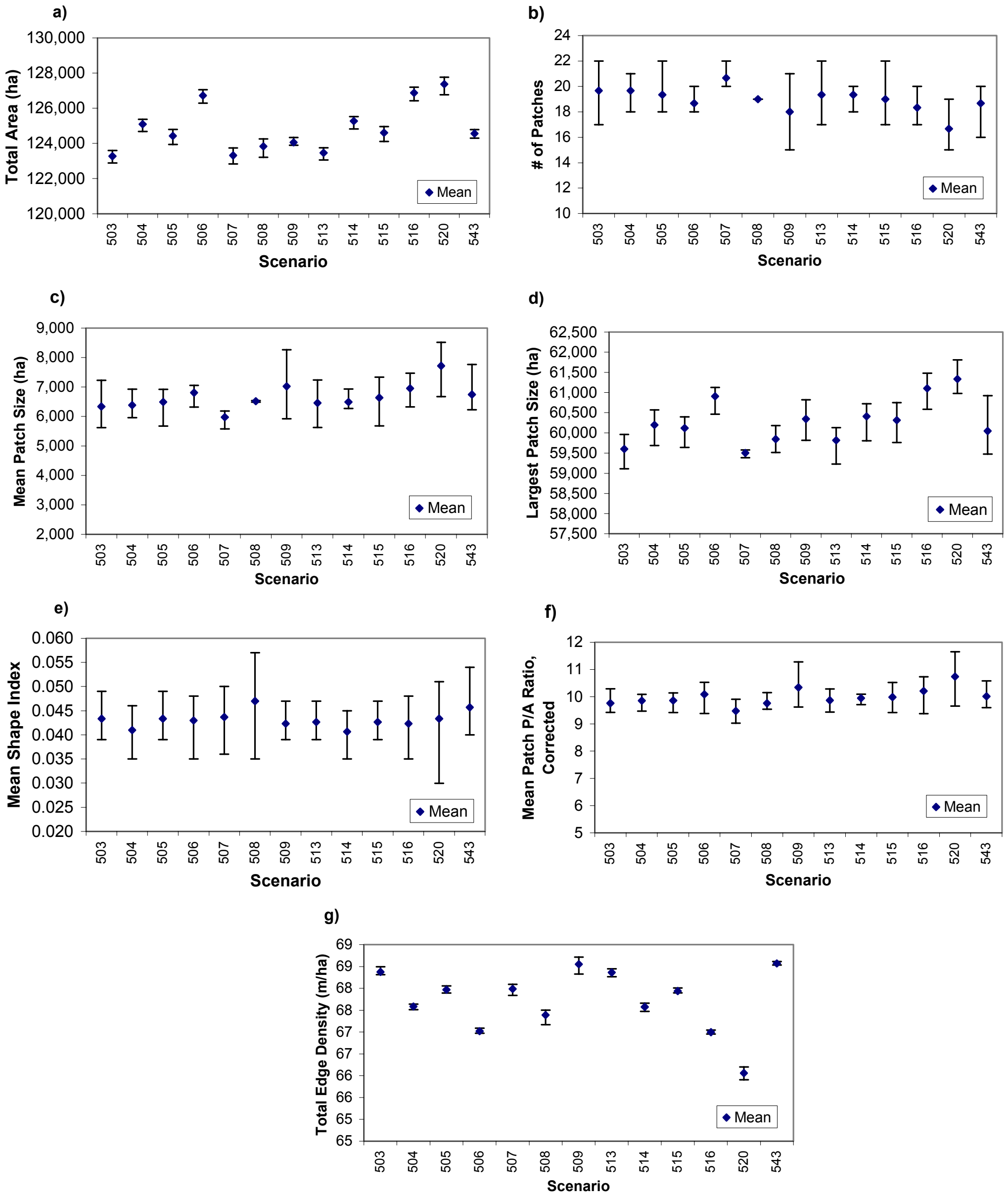

Figure 4—Values of wildland habitat landscape metrics for three iterations of the General Plan scenario (503) and alternatives (504-543). a) total area, b) number of patches, c) mean patch size, d) largest patch size, e) mean shape index, f) mean patch P/A ratio, corrected, and g) total edge density.

One of the iterations for scenario 508 has the highest mean shape index of all scenarios (0.057) but another iteration of 508 has the second lowest (0.035). Neither scenario was effective at maintaining the north-south connection (*figs. 3e, 3f*).

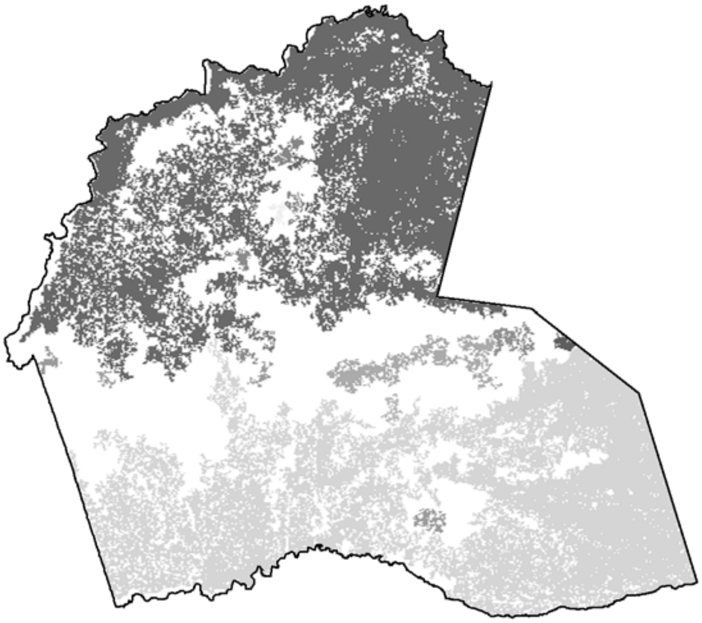

Figure 5—Map of wildland habitat after full buildout for parcel acquisition scenario (543).

General Plan Alternatives—"Kitchen Sink" and Planned Acquisition

Given that scenarios 504-516 were ineffective at increasing wildland habitat retention over the General Plan scenario or at maintaining the north-south connection, we tested two additional approaches. Scenario 520, dubbed the "Kitchen Sink" scenario, combined all of the most restrictive policies yet tested – 50 m stream buffers, 40 percent slope restriction, oak canopy retention for all developable land regardless of restriction status, plus clustering as per scenario 508 (B = 14 percent, C = 98 percent) (*table 1*). In contrast, Scenario 543 took a completely different approach leaving all original General Plan restrictions intact but expanding the area of non-developable land by restricting select parcels from development in key areas of concern. This scenario simulates a planned acquisition approach through the use of easements and/or outright purchase of development rights by the county. We selected several vacant parcels in the Indian Creek canyon area where it crosses Highway 50 between Placerville and Shingle Springs in an attempt to reconnect the northern and southern portions of wildland. In those selected parcels, we only restricted development on oak pixels and areas within 50 meters of oak pixels. This left some parcels still potentially developable.

As expected, scenario 520 retains the highest mean total area (127,376 ha) of wildland because it restricts the greatest area of land from development (133,217 ha) (*table 1*). Mean number of patches (16.67) is the lowest for all scenarios and subsequently mean patch size (7,721 ha) is the highest (*fig. 4*). Mean largest patch size (61,332 ha) is also the highest of all scenarios. Shape complexity does not decrease, however. Shape index is the same (0.043) as the General Plan scenario and mean corrected patch P/A ratio is the highest of all scenarios (10.74). In contrast, mean total edge density is the lowest of all scenarios (66.1 m/ha). Scenario 520 also does not come close to maintaining the north-south connection (*fig. 3l*).

As we made no attempt to preserve amount, but rather configuration, of wildland, scenario 543 only preserves an average of 1,296 more hectares than the General Plan (mean total area = 124,563 ha) and actually has slightly more average patches (20.0) and a smaller mean patch size (6,229 ha) (*fig. 4*). However, mean shape index is the second highest for all scenarios (0.046) while mean corrected patch P/A ratio is only slightly better than the General Plan (10.013). Mean total edge density is the same as the General Plan (68.57 m/ha). Most importantly, however, scenario 543 comes the closest of all scenarios to maintaining a connection between the northern and southern wildland patches (*fig. 5*).

Discussion

Our study demonstrated that the General Plan for El Dorado County will not allow the county to become one giant suburban subdvision. The General Plan allocates 43.0 percent of private land to development in the 1 unit/5 acre to 1 unit/40 acre density range (LDR and RR). Moreover, only 4 percent of the existing oak canopy will actually be removed by, or converted to, development. However, the configuration of this development is of concern as full buildout could force as much as 40 percent of the County's existing *wildland* oak woodlands into *marginal* or *urban* habitats. When counties are faced with such impacts, a popular mitigation approach is to implement prescriptions in the General Plan that regulate, and/or limit, how and where development can occur (e.g., stream setbacks, slope restrictions, etc.). However, such prescriptions can only apply to development that will undergo discretionary permit review, that is, parcels that have yet to be subdivided to the smallest allowable density in the General Plan. In the case of El Dorado County, 31 percent of *vacant* land that is *open to development* in the county (86 percent of parcels) had been subdivided prior to the adoption of the General Plan and is therefore not subject to these prescriptions. These parcels only require ministerial review (i.e., a building permit) before construction can occur. To impose a restriction that would regulate where development could occur in those parcels would require a county-wide ordinance. Our model allowed us to test both alternative General Plan prescriptions and county-wide ordinances. The former had little effect decreasing wildland habitat loss or fragmentation over existing General Plan policies. We attribute this to the large portion of the county not subject to the prescriptions due to prior subdivision. Ordinances showed greater wildland retention over the General Plan but that increase was still small. Scenario 516, the most restrictive ordinance scenario, only preserved 3,610 hectares more wildland than the General Plan and made little difference to patch configuration, shape complexity or edge density. The political expense in implementing ordinance-type solutions would seem to far outweigh the potential ecological benefits to oak woodlands.

Clustered development is a popular prescription proposed by the smart growth community. By holding overall density constant for an area but decreasing the space between structures, less space is scattered between structures which could otherwise serve as habitat and perform other ecosystem functions. The perceived advantages are so great that in order to promote clustering, El Dorado County offers a density bonus for clustered development in the Low Density Residential category (5 - 10 acre parcels). We modeled two clustering scenarios allowing densities to increase to the Medium Density Residential level (1 - 5 acre parcels). Neither scenario improved wildland habitat condition over the General Plan and some metrics for scenario 507 (mean number of patches, mean patch size and largest patch size) were actually worse. The increase in density, and therefore the increase in the amount of land developed, offset any benefit that would be gained from clustering. Furthermore, clustering can only occur in *vacant* parcels *open to development with restriction* in LDR. This occurs only in a few small areas in the northern portion of the county.

Scenario 520, the Kitchen Sink scenario, employed the strictest policy restrictions we tested, plus clustering. Looking solely at the fragmentation metrics (*fig. 4*), this scenario offered the most improvement in wildland habitat condition over the General Plan. Yet when examining the maps, we did not notice any significant difference in wildland amount or configuration (*fig. 3l*). Most notably, the north-south separation was still very pronounced. Implementing county-wide ordinances which mandate 50 m stream buffers, 40 percent slope restrictions and oak canopy retention on all undeveloped parcels, plus requiring clustering in LDR, is highly unrealistic, not to mention, very politically expensive. Again, we contend that the political costs of such a scenario are probably greater than the ecological benefits.

Alternatively, we examined a limited parcel acquisition, or easement, strategy (scenario 543) for areas of concern which removes key parcels from the potential development landscape. One such area is the Indian Creek Canyon region. Here, a stringer of oak woodlands presently connects the northern and southern wildland patches. Although this scenario did not actually maintain the connection, several small patches do extend through the area indicating that the concept has the potential to maintain this critical corridor. This area of the county is highly desirable for development, therefore making this scenario potentially fiscally expensive. However, unlike the ordinance approach, an acquisition approach would encounter fewer stakeholders directly and would offer owners compensation for the loss of development rights on their property. Involving private conservation groups or land trusts could greatly reduce costs to the public sector.

Rural residential development erodes habitat quality much more than habitat extent, requiring a more nuanced approach to assessing impacts than when natural habitats are simply removed or paved over. At these low densities, we were unable to use polygons of housing density to determine the relationship of naturalness to density. At certain scales, the landscape still looks much as it once did. Rather, we modeled the real impacts of site alteration which required an entirely unique set of variables and characteristics such as determining the exact footprint of development (e.g., Do lightly used roads count? Do outbuildings?) and establishing the sphere of influence from a structure (e.g., How far from the structure is natural vegetation disturbed? How far does sound travel? What impact does it have? What influence do pets have and at what distance?). We can easily adjust these variables in our model to examine their sensitivity and ability to assess other issues besides wildland connectivity such as impacts to specific species habitat requirements, watershed degradation from increased sediment generation, and changes in wildfire probability due to vegetative fuel alteration. Most people can agree that high density urban and suburban development do not provide much high quality habitat for most species, but seldom can stakeholders, land managers, public officials, or even scientists agree on the thresholds or the degrees at which rural development begins to impact the landscape. As more of the landscape of California transitions from large extents of wilderness owned by relatively few private individuals to a landscape divided up amongst thousands of owners regularly dotted with houses every few thousand feet, understanding these impacts and enacting policies that are effective, fair, and feasible become ever more important and challenging.

Future Directions

One aspect of development and conversion of natural land cover that we have not addressed is agricultural expansion. In El Dorado County this primarily involves vineyards. Agricultural expansion has the potential for far greater impact to habitat extent and connectivity than residential development as a greater area of land in larger contiguous patches is generally more greatly disturbed. Agricultural expansion can also be more difficult to predict. Heaton and Merenlender (2000) have developed a model to determine site suitability for vineyard expansion in Sonoma County which could be adapted for use in El Dorado County.

More investigation of the effects of riparian corridors on habitat connectivity is needed, including the effectiveness of stream setbacks and the development of methods to characterize linear features, as opposed to the two dimensional patch features analyzed here.

Better knowledge of the likelihood of development would enhance our ability to tailor solutions to specific areas of concern. The incorporation of economic models of development such as Johnston's UPLAN (2001) and Landis's CURBA (1998a, 1998b) would provide more realistic future scenarios as well as the ability to model development in stages over time rather than only at full buildout as we have done. Implementing other constraining factors to development such as water availability and habitat conservation plans could also improve our predictions of future development.

Conclusion

Fine-grained spatial models with highly detailed datasets are required for evaluating impacts of development on ecological, economic, or social systems at the local level. Such large-scale, high-resolution models also enable stakeholders to more easily relate the data portrayed on maps to their perception of the landscape in which they live. However, most site-specific models of development have been created for dense urban areas, using complex economic formulas of land value and empirically derived patterns of past development trends. These models prove less than reliable at predicting low-density development of the rural ranchette variety which is now so prominent in the Sierra foothills and which has such great impact on habitat quality. We have developed a model that is both fine-grained and capable of predicting potential rural ranchette development and its impacts. Moreover, by having a tool that can operate under various assumptions and constraints, we can actually test a proposed solution's efficacy at achieving a desired goal, which in this case is maintaining wildland connectivity. We have also used our model of predicting footprint of development to assess impacts of wildfire on future structure loss. Our explicit model of development could prove useful for studies of water quality and cumulative impacts for watersheds by incorporating elements such as sediment generation from road development, nutrient loading from septic systems, and conversion of natural land cover to impervious surfaces.

Existing land tenure (the historic parcelization of land) limits effective control of development by General Plan prescriptions that are only applicable when a parcel requires subdivision before development, thus leaving solutions that require large expenditures of political capital such as ordinances or downzoning. The political expense in implementing such solutions would seem to far outweigh the potential benefits. For El Dorado County, our study concludes that the most effective way to maintain wildland oaks in large contiguous patches would be a land acquisition program focused on those critical areas of connectivity, often referred to as habitat corridors. More importantly, broad-brush, "best management practice" type solutions (i.e., the conventional wisdom) applied evenly across the landscape are not necessarily the most effective approach. Site-specific design may be a more effective tool in minimizing negative impacts of development than generic policy prescriptions. "Good" policy should be a process by which better analysis of the problem leads ultimately to better design of the solution.

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Oak Management by County Jurisdictions in the Central Sierra Nevada, California[1]

Richard R. Harris[2] and Susan D. Kocher[2]

Abstract

We evaluated county planning policies and procedures to determine what protection is provided to oak woodlands during the land development process. We selected three Sierra Nevada counties to do a pilot assessment: El Dorado, Placer and Madera. The assessment methodology included three components: 1) analysis of county plans, policies, guidelines, and ordinances to determine if oak woodland management is addressed and if so, how; 2) analysis of development case studies to document the planning process used to conserve oak woodland; and 3) field evaluation of typical oak management activities at the site scale. The counties vary widely in the extent and detail of their oak protection policies and in how they approach oak conservation at the landscape, stand and site scales. In particular, conservation and protection measures often focus on individual trees or groves at the expense of larger woodlands. At the site scale, we observed both ineffective protective measures as well as innovative approaches to site planning that resulted in the protection of oak groves or specimen trees. The results of our assessment should prove useful to county and local agencies interested in oak conservation. This research also provides an assessment methodology for a statewide evaluation of county policies and procedures.

Introduction

In California, there is presently a great deal of controversy concerning the protection of native oak woodlands. It is certain that the status and treatment of oak woodlands varies from place to place in the state. In the absence of any comprehensive statewide oak specific regulations, conservation and protection of oak woodlands falls to county and city governments. State (or Federal) regulatory requirements usually only come to bear when other resources, such as streams, wetlands and endangered species, are also involved.

The University of California, Integrated Hardwood Range Management Program (IHRMP) approached the authors and requested that we conduct a study of the effectiveness of county management of oak woodlands in the Sierra Nevada. We were asked to use a methodology that we had applied previously to assessments of county management of anadromous fish (Harris and Kocher 1998, Harris and others

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[1] An abbreviated version of this paper was presented at the Fifth Symposium on Oak Woodlands: Oaks in California's Changing Landscape, October 22-25, 2001, San Diego, California.

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2000). The results of that research are summarized in this paper and presented in greater detail in a report to IHRMP (currently in review).

This research was not intended to be definitive but rather, to indicate through a pilot study, what the main issues are and what additional research might be conducted. It is a case study approach involving only a few counties. It is probable that conditions in other counties are quite different than the ones we studied. However, we do feel that some of the major issues related to local management of oak woodlands have been determined. The results should be useful to researchers and policy makers wishing to gain a better understanding of the constraints to effective oak woodland conservation in the foothill counties.

Methods

The study area for this research was El Dorado, Placer and Madera Counties in the California Sierra Nevada foothills. Research goals were: 1) to determine how existing policies, regulations, California Environmental Quality Act (CEQA) process, mitigation measures and land use practices are used to minimize the adverse effects of county-regulated or funded activities in California oak woodlands. The primary focus was on land development. The scope of review spanned planning and approval processes through implementation; and 2) to determine the degree to which the approaches to oak management in the counties are consistent and effective. Consistency was evaluated through tracking policies and procedures and their implementation during project approval processes and effectiveness was evaluated by field studies of post-development conditions.

County-regulated activities may affect oak woodlands in different ways at different scales. To provide an orientation for our study, potential impacts on oaks were classified as either direct or indirect occurring at the individual tree, stand/grove, or landscape scales. A direct impact was defined as partial or total removal of trees, patches of trees or large-scale clearing. An indirect impact was defined as an alteration of environmental (e.g., soil or water status) or ecological (e.g., species composition or stand structure) conditions that would affect oak health, vigor or life span. We operationally defined a tree's impact area by its crown as projected onto the ground surface (i.e., within its drip-line). A stand or grove was defined as a vegetation patch dominated by native oaks and generally less than a few acres in size. The landscape scale was defined as a relatively large patch (tens of acres) of oak woodland with continuous crown cover (more than 50 percent cover). Under these definitions, an oak savanna would normally qualify as individual trees but could be called a woodland, depending on its density. Groups of oaks separated in space by other vegetation types or by development were treated as groves. An oak woodland-dominated landscape could have one or more of several vegetation types found in the study area, including mixtures of oaks, pines and shrubs.

We met with county planning and public works staff and they indicated that the primary activities, which affect oaks within their jurisdictions, were residential, commercial, and recreational development (golf courses). They also expressed concern about road construction and reconstruction projects. Therefore, our work focused on these activities in oak woodlands.

After we determined the important activities, we inventoried all of the policies and procedures that each county uses to prevent or reduce potential effects on oak woodlands. These tools included formal adopted policy (e.g., general plans, subdivision, zoning and other ordinances, etc.) as well as planning and environmental review procedures as documented in CEQA reports, planning reports and permit conditions. We also identified practices used in the field, such as methods used to protect oaks at construction sites.

After conducting the inventory we reviewed all applicable plans and policies to determine how oak woodlands were addressed (planning policy analysis). This was followed by an analysis of how policies were applied to projects during the approval process and environmental review (development processing). We then evaluated implementation of mitigation measures at specific sites (field assessment). Essentially, we followed policies from their origin in plans and ordinances through the development review process to the ground. Case studies and field sites were jointly chosen by county staff and UC researchers. Field site inspections were conducted by a team consisting of county staff and UC researchers. Field observations were recorded on standardized forms.

The products of this research are: 1) an inventory of policies and regulations in place for protecting oak woodlands; 2) a qualitative evaluation of the adequacy of the project review process in protecting oak woodlands; and 3) a qualitative evaluation of mitigation measures used in the field to protect oak woodlands. These products can be used as the basis for proposing modifications of procedures or additional procedures to bolster existing mitigation tools.

Results

Planning Policy Analysis

Every county's general plan and ordinances have developed over time in place and each uses different approaches for conservation of natural vegetation. The general plans for all three counties advocate conservation of oak woodland resources for their wildlife habitat values. They also recommend that new developments preserve natural woodlands to the maximum extent possible. However, the methods used to achieve these goals, the types of projects that are regulated, and the scales at which efforts are focused are different in each county.

Placer County

In Placer County, the General Plan, Tree Protection Ordinance and Placer Legacy program together establish oak conservation programs at the tree, stand, and landscape scales. As previously mentioned, the General Plan contains substantive language aimed at protecting oak woodlands. Placer County's Tree Protection Ordinance requires virtually all development projects (and landowners) to avoid or mitigate tree removal. A developer must submit information for all trees on the site and based on this information, specific conditions are imposed for tree retention and mitigation. Approval for tree removal requires in-kind replacement or payment into the Tree Planting Fund. Proposals for replanting or relocating trees require assurances of maintenance and survival. The Ordinance lists standards that must be used to protect retained trees during construction within 50 feet of any development activity. A deposit may be required to insure tree preservation during grading and damage to trees may incur a financial penalty. Preservation devices such as aeration systems, oak tree walls, drains, special paving and cabling systems may be required.

The Placer Legacy Program is an initiative to preserve oak woodlands at the landscape level. The Program acknowledges that foothill oak woodlands have little regulatory protection and directs the County to preserve oak woodland through a variety of means. Areas of oak woodland with particularly high ecological value have been identified throughout the County and preservation mechanisms such as conservation easements, agency land trades, riparian setbacks, and fee title acquisition have been proposed for them. Direct acquisition is recommended in areas of relatively intact oak woodlands in the northern, less developed parts of the County's foothill region. At the present time, funding for implementing the Placer Legacy Program has not been secured.

El Dorado County

In El Dorado County, canopy retention and open space requirements found in the General Plan are the basis for oak woodland conservation. The canopy retention standards require discretionary projects on parcels having oak woodland canopy cover of at least 10 percent to retain or replace the existing tree canopy on an area basis, e.g., if one acre of trees is removed, another must be planted. In locations with an existing canopy cover of 80 to 100 percent, 60 percent of the existing canopy must be retained or replaced. Retention requirements increase as canopy cover decreases, e.g., for sites with less than 20 percent canopy cover, 90 percent of the existing canopy must be retained or replaced. Proposed Oak Woodland Guidelines would add a requirement to discretionary projects for a woodland conservation plan that describes oak woodland conditions before and after the proposed project.

The County's General Plan also emphasizes the use of clustered development to retain natural vegetation. Planned development projects, including all subdivisions that create more than 50 new lots, must set aside at least 30 percent of the project area as open space land. These open space areas can be used to meet canopy retention requirements.

Standards for protection of retained oaks are established in the El Dorado County Design and Improvement Standards Manual, which prohibits disturbance or changes within the drip-line of any oak tree during construction. This is a guide, not an ordinance.

Madera County

In Madera County, the General Plan calls for protection of oak woodlands. The main vehicle for enforcing these provisions is the CEQA/environmental review process. Several discretionary projects we reviewed during the field assessment of practices contained what appeared to be effective oak mitigation measures that were imposed by the County during the environmental review process. However, most discretionary projects and all ministerial projects visited did not appear to have been required to mitigate impacts on oaks.

The Madera County Board of Supervisors has adopted a set of voluntary guidelines developed by the Coarsegold Resource Conservation District to assist landowners in the management and stewardship of private property. These guidelines list specific standards and measures for conservation of oaks and oak woodland during building, agricultural operations, and fire safety clearing, and to promote wildlife habitat. We did not determine whether or not these guidelines have an effect on oak woodland management by private landowners.

Development Review Process

Eight case studies, including residential, commercial and golf course developments were reviewed to determine the environmental and planning review procedures followed by the counties and the degree to which they addressed effects on oaks at the individual tree, stand/grove or landscape level. Documents reviewed included Environmental Impact Reports (EIRs), staff reports, and approving resolutions, if available. Some of the projects were visited in the field as well and observations on them were recorded. Several conclusions were drawn from review and comparison of the case studies.

Generally, the scope and level of detail with which projects were reviewed varied with their scale and degree of public controversy. Involvement of outside state or federal agencies, such as the Department of Fish and Game or US Fish and Wildlife Service, and presence of environmental or ecological resources other than oak woodlands, such as streams or wetlands, also influenced the degree of environmental analysis conducted. General plan and other policies regarding oak woodlands were used in the planning and environmental review process to establish criteria for assessment and mitigation. However, there were few ecological criteria applied to the evaluation of oak woodlands unless other important resource values were associated with them, such as endangered species. For example, standard plant community nomenclature was not used to describe oak woodlands.

The assessment of existing oak woodland was done differently in each case (tree surveys, canopy surveys, qualitative descriptions) and by different people (general environmental specialists, arborists, foresters). In some cases, detailed descriptions of individual trees were provided but there was no description of the stand or the landscape. This is partly a consequence of the different policies and procedures used in the counties: Placer County requires tree surveys, El Dorado County requires canopy analysis and Madera County has no standardized assessment methodology.

In accordance with different policies, different definitions were used for a "tree," e.g., 3 inches diameter breast height (dbh), 6 inches dbh, 24 inches dbh, and for tree impact areas, e.g., 50 feet to 200 feet from construction activities. Different methods were used for assessing impacts, e.g., analysis of changes in canopy, evaluation of individual tree losses, areas of habitat lost or qualitative only. Generally, no quantitative methods for detailed ecological characterization of oak groves or landscapes were used. Impacts on trees, rather than groves or landscapes, were the main focus of analysis and mitigation.

Different standards were proposed for protecting trees from construction or long-term impacts, e.g., within drip-line, one foot from drip line, five feet from drip line, 10 feet from drip line. These were sometimes, but not always consistent with county standards. Different methods for mitigating or preventing losses were proposed as well, e.g., avoidance, tree planting, open space easements, etc. None of the case studies provided documentation that tree planting can effectively mitigate losses at the stand or landscape level. Different planting guidelines and maintenance requirements were recommended and responsibilities for implementing mitigation varied, e.g., individual homeowner, homeowners' associations, county, developer.

The methods proposed to preserve areas of oak woodland varied (e.g., open space easements, open space parcels, large lot sizes), as did their proposed means of management and protection, e.g., fenced or not fenced, subject to vegetation management or not, etc.

The question of the sustainability of small patches of preserved woodland within urbanized landscapes was not addressed in any case studies. For example, in subdivision designs that created several open space parcels, the issues of use by residents were not often addressed. In some open space parcels, we observed vegetation management occurring that appeared to be in violation of restrictions on use.

For planting projects or open space preservation, monitoring requirements varied, as did measures of mitigation performance, e.g., tree survival rates, canopy replacement goals, etc. No information on the effectiveness of off-site mitigation methods, including tree planting funds, mitigation banking and planting at off-site locations were presented to justify their use in replacing lost resources. Long-term vegetation management impacts on planted or preserved oak woodlands were not often considered, e.g., roadside vegetation management, clearing for fire protection.

We found that within a county, the planning and environmental review process used for case studies was similar although the results differed depending on project type and scale. However, among counties, the procedures varied greatly. Our overriding conclusion was that there was substantial variability in approaches to resource description, impact assessment and mitigation. This reduces the certainty of consistent protection throughout the region. Although it was clear that some projects did have designs that would protect at least some resources, this was not true everywhere. One important consequence of the inconsistent framework for analysis and protection is that oak woodlands of county-wide or regional significance cannot be identified during the project review process. Each project is dealt with in isolation from others and cumulative impacts cannot be assessed.

Field Assessment of Practices

Thirty-one development sites were formally evaluated in the three counties and many more were observed in passing. The activities observed and the practices applied appeared to be representative of the range of projects in the counties, but the sample was not intended to be statistically significant. The projects included 15 residential developments, nine commercial developments, four golf courses and three road construction projects.

Residential Development

The fifteen residential developments ranged widely in their design characteristics, size and degree of regulatory complexity. Generally, all but one of these projects involved some amount of tree removal to enable construction of roads, clearing of building sites and house construction. The number of trees removed was a function of the density of the woodland affected and intensity of development, i.e., amount of grading and size and density of building sites. The mitigation measures applied to tree removal were both voluntary and regulatory. They included avoidance through site planning and restrictions on building site locations through definition of building envelopes on recorded maps. Some of the projects were required to quantify the number of trees removed and replace them either on or off site. Plantings observed were opportunistic, and the planting methods and maintenance practices varied. Most of the projects also involved fragmentation at the stand level. This included removing trees and understory and reducing stands to isolated residual trees. To achieve mitigation in some cases, groves were preserved in association with open space or riparian easements. In a couple of cases, fragmentation also occurred at the landscape level. These were large developments in extensive, dense oak woodlands where roads and building sites created multiple openings or large clearings. No specific measures to avoid landscape-level fragmentation were observed.

At every site where construction was underway and at some completed projects, construction or use-related damage to residual trees was observed. This included machinery operations under trees, grading, construction and trenching beneath trees, machinery damage to stems and branches, and equipment storage beneath trees. Permanent changes observed beneath trees included housing foundations, landscaping, paving and grading. In some cases, rather detailed mitigation measures for avoiding such damage had been recommended but implemented only in part or not at all. In other cases, there were no specific measures applied and avoidance was voluntary but inconsistent.

At three sites extensive clearing for fire protection (i.e., creation of “defensible space”) was observed. In these cases, complex multi-storied oak woodland stands were cleared of understory shrubs and trees and thinned. The resulting condition was individual trees without overlapping crowns and with open understory or bare ground underneath. There was an attendant loss of species and structural diversity. This practice is actively promoted and no mitigation measures to prevent it are applied.

Commercial Development

We reviewed nine commercial and industrial developments, including some churches. Most were conditional use permits on existing parcels involving various levels of regulatory review. The nature of commercial or light industrial development is such that site coverage is greater and buildings are larger than residential development. As a result, larger areas and perhaps, a greater proportion of the site are subjected to clearing and construction impacts. In a few of the reviewed cases, trees were avoided through site planning, but mostly trees in the path of development were lost. Mitigation measures applied to avoid trees included cut-outs in parking lots or creation of “islands” with trees on them. In four cases, stands were either removed or fragmented into individual trees. On one site, a stream and associated oak riparian zone were relocated from the center of the parcel to the periphery to allow construction of a parking lot. Mitigation measures applied to groves included their protection as undeveloped open space and replanting of trees pursuant to ordinances. Some residual trees suffered construction-related damage or had permanent changes beneath their crowns, such as paving. In applicable cases, landscaping and irrigation beneath retained oaks were minimized. There was evidence of involvement by an arborist or forester only on one site.

Road Projects

Three road reconstruction projects were evaluated. All of these involved widening existing roads within defined rights of way, and options for site planning to avoid oak losses were limited. The primary impacts were losses of individual roadside trees but in one case, a grove will be lost due to an intersection re-alignment. Mitigation measures included replanting trees either within the road right of way or at off-site locations or contribution to a tree planting fund. The main limitation to mitigation was availability of sites for replacement plantings.

Golf Courses

Four golf courses were evaluated. In the three golf courses that were constructed in relatively dense oak woodland, the landscape was reduced from continuous canopy to individual trees, lines of trees and isolated groves. In the other case, the golf course was situated in a floodplain between a river channel and overflow channel. It may have been riparian forest in the past but had been cleared long before the golf course project. Treatment of retained trees within or adjacent to groomed areas varied. In some projects or parts of projects landscaping and irrigation were restricted in the vicinity of retained trees. In other situations, no restrictions were evident. Some retained trees were located within fairways and subject to all grooming and irrigation practices. Results varied. No ill effects were observed in some retained trees while others had clearly suffered or died. Mitigation measures for lost trees included replanting on site, in or around fairways, with and without turf and irrigation underneath. On one site, trees planted in fairways where they were irrigated and fertilized were growing extremely well. There were also restrictions placed on grading or paving beneath retained trees. Some groves were retained as open space and on one site, 300 acres were preserved, mitigating landscape-level fragmentation to some extent.

Discussion

Our review showed that Placer County has the most comprehensive set of policies addressing oak woodland conservation. In Placer County case studies, there was a clear linkage between policies and development processing. However, lack of funding for the Placer Legacy Program may prevent effective conservation at the landscape level. El Dorado County’s main tool for oak conservation, requirements for canopy analysis, provides some benefits that a tree protection ordinance does not. However, in the El Dorado County case studies and in the site review, some projects had high enough initial oak woodland densities so that the canopy analysis requirement was not triggered. Also, unlike Placer County’s tree ordinance, which applies to any tree removal, the canopy analysis procedure only applies to discretionary projects. Madera County has the least assertive policies but it implements oak conservation through the CEQA process. The scale and visibility of a project and the presence of resources other than oak woodlands, especially wetlands and riparian zones, had definite effects on the intensity of environmental review and the quality of mitigation measures applied.

In all counties, the site reviews indicated that implementation of mitigation measures was not consistent or effective. In every county, conditions on sites undergoing development appeared similar. That is, oak protection at the site level is ineffective. The most significant impacts observed were construction or use-related damage to residual trees. According to County staff, the ubiquitous damage to residual trees was due to several causes including a lack of coordination between planning and building departments regarding conditions on development permits, lack of enforcement or monitoring, field judgment calls on grading or building siting by building contractors and pure accident.

On several field sites in which open space parcels had been preserved, they appeared to be reasonably planned and potentially effective in protecting resources. In the long term, the management of these open space areas will determine their sustainability. Management guidelines and implementation varied from site to site.

Practices used for planting of new oaks and management of residual oaks varied as did the observed results. For example, we observed places where oaks were subjected to irrigation and had died and other places where they were irrigated with no apparent ill effects. Several different planting methods were observed using differently sized planting stock, from pre-sprouted acorns to 15-gallon container stock. Better practices for regenerating and managing native oaks are probably needed to obtain more consistently successful results.

The practice of planting to mitigate losses is itself questionable. We observed planting oaks underneath existing woodlands, planting in median strips and along property lines and planting on cut and fill slopes. These plantings were often aimed at mitigating losses of stands or groves. They would function ecologically as replacements for groves only in a few cases. Off-site planting, in general, is constrained by the availability of suitable planting sites.

Finally, there is an inherent conflict between protecting and enhancing the biological diversity of oak woodlands and the implementation of strict “fire-safe” development guidelines. Further study of this would be warranted, especially in view of the assertive efforts being taken to reduce fire hazard. The trade-off for marginal reductions in fire risk may be significant decreases in the biological diversity of oak woodlands.

Conclusions

Our conclusions, presented below, are provided with two goals in mind: achieve better regional consistency in protecting oak woodlands and achieve better mitigation effectiveness.

There appears to be a need to improve the methods used to evaluate and assess impacts on oak woodlands. Descriptions at multiple scales are needed if the ecological significance of specific oak woodlands is to be understood by decision makers. Better ecological descriptions would enable better predictions of the consequences of their fragmentation or loss.

Improving protection of oaks on construction sites appears to be as much an educational issue as a regulatory one. In particular, there appears to be a need to provide a better understanding of oak protective measures to construction workers. The need for additional regulatory tools might be avoided if better educational programs are developed.

Better information on management of oak woodland open spaces should be provided to the many entities that are assuming responsibilities for their sustainability. This is not being adequately addressed in either CEQA process or in conditions on developments. The future ecological integrity of many oak woodlands is at stake.

There is an apparent need for dissemination of information on "best management practices" for oak planting and maintenance. These may vary considerably by species and site. There is a multitude of practitioners who could benefit from this information.

Additional research or monitoring is needed to determine if on-site or off-site compensatory planting are suitable mitigation measures for losses of mature oak trees and stands and for landscape fragmentation.

Research is also needed on the ecological and environmental effects of "fire-safe" treatments and fuels management on oak woodlands.

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Harris, R. R.; Kocher S. D.; Kull, K. M. 2000. **Effects of county land use policies and management practices on anadromous salmonids and their habitats: Sonoma, Marin, San Mateo, Santa Cruz and Monterey Counties, California.** Department of Environmental Science, Policy and Management, University of California, Berkeley; 54 p + appendices.

Inconsistent Application of Environmental Laws and Policies to California's Oak Woodlands[1]

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Abstract

We examine inconsistencies in the application of environmental laws and policies to California's oak woodlands and associated resources. Specifically, large-scale vegetation removals receive different levels of environmental oversight depending on location, tree species, and the final land use designation. Hence, situations arise where the scale of impacts to the ecosystem can be similar but are regulated differently depending on forest type. These inconsistencies can lead to environmental impacts, confusion, and inherent inequities among private landowners. The historical, institutional, and political climate under which the Forest Practice Act and California Environmental Quality Act were developed has resulted in the dichotomy that oak woodlands face. We use agricultural development in California's North Coast watersheds and the potential impacts to anadromous fish conservation to illustrate the problem. Examining this scenario provides a better understanding of how and why oak woodland resources continue to diminish in some parts of California. We also explore improvements that should be made to provide environmental review and full disclosure to ensure fair and equitable protection of natural resources and consequences for landowners. These include more emphasis on consistent environmental review, ecosystem management, watershed level planning, and protection of natural communities in addition to individual tree protection.

Introduction

Oaks span across many of California's diverse climatic zones and define the landscape for its many residents. California oak woodlands are primarily held in private ownership, and many historic and modern day land-uses have reduced their biological integrity. In 1909 botanist Willis Linn Jepson states: "In some regions where the horticultural development has been rapid or the needs of an increasing population urgent, extensive areas have been cleared to make room for orchards or gardens, and scarcely a [valley oak] tree remains to tell the story of the old time monarchs of the soil, in other regions the destruction has not been so complete" (Pavlik and others 1991). Walter (1998) provides an overview of how past land-use practices have changed the landscape of California so dramatically that in some cases counties "have lost their natural heritage" and only retain remnants of their past biological richness.

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[1] An abbreviated version of this paper was presented at the Fifth Symposium on Oak Woodlands: Oaks in California's Changing Landscape, October 22-25, 2001, San Diego, California.

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Oaks continue to be removed for urban and agricultural development despite modern environmental protection policies (Jensen and others 1993). The removal of oak woodlands is not directly regulated by the State, but there are applicable State, local, and more recently Federal policies and statutes that tangentially relate to oak woodland resources. This is dramatically different from the State's current role in overseeing tree removal and regeneration on conifer-dominated sites. This difference has resulted in a dichotomy of social and environmental policies produce an inconsistent level of protection for natural resources that rely on the natural continuum that exists between these forest types across the landscape. To illustrate the problem, we present a case study from North Coast California where anadromous fish conservation is essential and forest conversion for vineyard development is occurring in both woodlands and timberlands. Since many environmental protection policies revolve around the potential application of the California Environmental Quality Act (CEQA), we elaborate on its relevance to this discussion.

At the State Level

The State Board of Forestry is recognized as having the legislative authority to regulate both privately owned conifer and oak woodland forest types. With the passage of the Z'Berg-Nejedly Forestry Practice Act of 1973 (FPA), the Legislature reorganized the Board and concomitantly expanded its powers and responsibilities. The FPA, in combination with the Forest Practice Rules (FPR) set forth by the Board, are designed to identify and mitigate any potential negative impacts from the harvesting of timber as a requirement of the California Environmental Quality Act (CEQA). Prior to the harvesting or clearing of commercial tree species for other land uses, a Timber Harvest Plan (THP) or a timberland conversion permit respectively, must be prepared by a Registered Professional Forester (RPF), and approved by the California Department of Forestry and Fire Protection (CDF). These serve as *functional equivalents* of an Environmental Impact Report (EIR) under CEQA.

Historically, the Board has focused its regulatory authority on those lands capable of producing "commercial species," conifers deemed economically important under the FPA and some hardwood species growing on timberland. It chose to support an educationally based program for oak woodlands. Only under specific circumstances are pre-determined oak species and other hardwoods recognized by the Forest Practice Rules. In all other situations, if oak species are removed from lands not designated as timberlands for purposes other than development they are not afforded protection under the FPA, thereby, not categorically subject to CEQA. This has led to some confusion because under specific circumstances species such as black and Oregon oaks (*Quercus kelloggii* and *Q. garryana*) are recognized as commercial species and are regulated by CDF while in others circumstances they are not. In this case, the economic value of the surrounding trees determines which parcels receive government oversight prior to oak removal, ultimately resulting in an environmental review process that excludes the intrinsic values associated with native trees such as oaks occurring outside of commercial timberlands.

At the Local Level

The educational path for California oak protection was established with the creation of the University of California's Integrated Hardwood Management Program

(IHRMP) in 1986. In 1993 the Board delegated to the IHRMP the responsibility of assisting counties in the development of locally based conservation strategies for oak woodlands in lieu of a statewide regulatory program. In response to this directive, counties have developed a wide array of resolutions, ordinances and voluntary efforts through a variety of committees, Board of Supervisor actions, resolutions and initiatives.

This decentralized approach to oak conservation has promoted a variety of schemes that have been developed, modified and implemented throughout the oak region of California in an attempt to address both oak woodland aquatic and upland issues. A variety of resolutions (e.g., Tehema, Shasta, Madera Counties), various ordinances (e.g., Sonoma, Lake, Santa Barbara), evaluation committees (e.g., Lake, Madera), monitoring efforts (e.g., El Dorado) and ballot measures (e.g., Santa Barbara) have been initiated to address a wide array of oak conservation issues. In many instances, the adopted mechanisms have focused on a single resource issue such as tree protection rather than a comprehensive strategy. A recent newspaper article elucidated how local tree ordinances to protect heritage oaks in developed areas have proliferated, and sometimes results in a burdensome level of oversight for many small landowners (Purdum 2001). Additionally, it is becoming apparent that many of these local initiatives lack adequate monitoring mechanisms capable of evaluating their effectiveness.

In the presence of continued land-use practices that alter habitats, counties are now faced with the reality of trying to prevent landscape scale impacts to oak woodlands without the benefit of sufficient resources. In a few cases, the responsibility of compliance with oak protection policies lays with a local Resource Conservation District or an ad hoc committee. In almost all other cases, county planning departments have this responsibility. Due to limited financial resources and expertise, it is difficult for counties to comply with existing federal and sate regulations such as the Endangered Species Act and the Clean Water Act, let alone implement an oak conservation strategy. Additionally, local government has a difficult time assessing natural resource loss in an unbiased manner because of political pressure from interest groups trying to avoid environmental regulation and associated costs.

CEQA and Cumulative Impacts

The primary tool available to local planners to mitigate negative impacts of development to the environment is CEQA. According to Fulton (1999) the primary role of CEQA is to address four functions.

- To inform decision-makers about significant environmental effects
- To identify ways environmental damage can be avoided
- To prevent avoidable environmental damage
- To disclose to the public why a project is approved even if it can lead to environmental damage.

CEQA has been one of the most hotly contested planning laws since its inception in 1970. The Little Hoover Commission (1994) chided CEQA process as "complex, lengthy, and costly, resulting in inconsistency and inequity." This report, which evaluated how CEQA was being applied through the Forest Practice Rules, emphasized that an important flaw in the CEQA process was its piecemeal approach of evaluating cumulative impacts from repetitive timber harvests within watersheds. Though cumbersome and often costly, the CEQA process is the only existing comprehensive system that can effectively review the environmental impacts of land-use.

By definition cumulative impacts are "two or more individual effects which, when considered together, …compound or increase other environmental impacts". Another way of stating this definition was established by the courts as "an analysis that assesses cumulative damage as a whole greater that the sum of its parts" (*EPIC v. Johnson* (1st Dist. 1985) 170 Cal.App.3d 604, 625 [216 Cal.Rptr. 502] because "the full environmental impact of a proposed…action cannot be gauged in a vacuum" (*Witman v. Board of Supervisors* (2d Dist. 1979) 88 Cal.App.3d 397, 408 [151 Cal.Rptr.866]. These cases established the precedent that an agency may not treat a project as an isolated single-shot venture in the face of persuasive evidence that it is but one of several substantially similar operations. It further recognized how unless cumulative impacts are analyzed, agencies tend to commit resources to a course of action before understanding its long-term impacts.

Undeniably, the evaluation of cumulative impacts from land-use projects is one of the most challenging issues facing resource managers and planners. A recent UC report evaluating cumulative watershed effects from timber harvesting points out the extreme difficulties of this task in the absence of a centralized database from which to make assessments. In this report, Dunne and others (2001) recognized the daunting task monitoring forest land-use practices to minimize cumulative impacts from repetitive timber harvesting plans even for a State agency such as CDF. Given the difficulty for an agency the size of CDF to monitor cumulative impacts, one could surmise the difficultly a county agency would have performing similar functions. Additionally, the Dunne Report was evaluating the current timber harvest process of repetitive harvest and replanting of timber resources that does not result in the conversion of timberland. This is quite different from the challenges facing local planners who are attempting to identify cumulative impacts to oak dependent environs from practices that result in the conversion and net loss of oak woodland acreage.

Migrating Fish and the North Coast Forest Continuum

Through a separate set of Forest Practice Rules, the Z'Berg-Nejedly Act recognizes the need for the protection of stream zones, soil stability, and cumulative effects during timber harvest. A recent independent scientific panel determined the level of protection for salmon was inadequate (Ligon and others 1999); and led to amendments for stream zone protection on timberland by the Board of Forestry. These policy changes were driven by the fact that populations of anadromous salmonids are in danger of extinction throughout the western United States.

Within California, tree removal to facilitate changes in land use have influenced the temperature, sediment load, and physical structure of rivers and streams, making them substantially less hospitable for these native fishes. Parts of Central and Northern California have Mediterranean-climate where populations of salmon and steelhead trout occupy watersheds dominated by hardwood rangelands and woodlands. In many North Coast watersheds salmon migrate through conifer-dominated drainages and ultimately complete their journey to their spawning areas in a predominately oak woodlands habitat type. After spawning juvenile salmonids will spend a significant portion of their early life stages in the oak-dominated portions of the watershed in preparation for their down stream migration to the ocean. While in this phase, juvenile fish are susceptible to degradation of either in-stream or near stream habitats. In fact, within a single and adjacent drainage that support the same population of fishes both conifer and hardwood dominated cover types exist *(fig. 1)*.

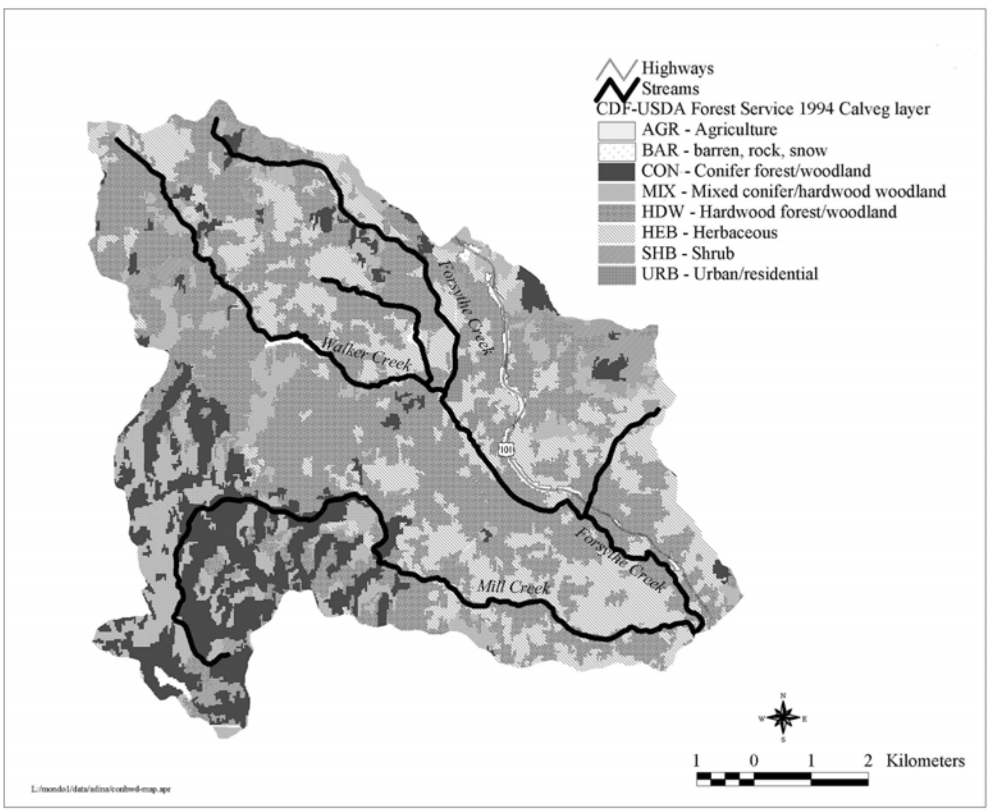

Figure 1—Walker and Mill Creek planning watersheds in the Russian River with vegetation cover types as mapped by CDF-USDA USFS 1994 Calveg are mapped to illustrate the forest continuum that exists between conifer and hardwood forests. Walker and Mill Creeks have historic records of steelhead runs, and Forsythe Creek once had coho and steelhead (CDFG 1920-2000 historic fish records). Agricultural conversion in the conifer dominated sections would fall under CEQA review as part of a conversion permit, while other areas are not likely to have "commercial species" and would not fall under any comprehensive environmental review.

Since the current oversight by the State is primarily restricted to a narrow definition of timberland, salmon are not protected to the same extent across their migratory pathway to and from natal spawning grounds and the marine environment. To illustrate the point, we can examine the Russian River, which has some mesic conifer forests, and many headwater reaches that run through oak woodland and shrub habitat. This same continuum between forest types exists throughout the northwestern counties of Sonoma, Mendocino, and Humboldt; in the Russian, Navarro, Eel, Klamath, and Smith River systems. In other parts of California a similar continuum exists with conifer dominated mountainous forests transforming into oak dominated types in drier or lower elevation sites within the same watershed, making the current division between conifer and hardwood forest types arbitrary when assessing impacts to watersheds, migratory species and ecosystem integrity.

Non-development activities (e.g. large-scale tree removal, road building, grading and recontouring) that result in the loss of oak forest cover are only subject to regulations surrounding streambed alterations and water quality issues. By contrast riparian areas designated as timberlands are afforded protection under the watercourse and lake protection clause of the Forest Practice Rules. The statute's explicit intent is to prevent the removal of "water, trees or large woody debris from a watercourse or lake, the adjacent riparian area, or the adjacent flood plain in quantities deleterious to fish, wildlife, beneficial functions of riparian zones, or the quality and beneficial uses of water" (FPA Article 6). The absence of a policy that recognizes the existence of the forest continuum including oak dominated forests establishes a double standard of environmental protection. Equally important is the fact that the burden of regulations is not shared equally among adjoining landowners with different forest types. Landowners with "commercial trees" are subject to the FPA at considerable expense if they want to convert the site (remove the trees), while those with only hardwood cover are not subject to the FPA. For this reason, in the North Coast, current forest policy does not adequately protect natural resources across the continuum that exists between conifer and hardwood dominated forest types and differentially impacts neighboring landowners.

Agricultural Conversions in North Coast Watersheds

An example of the environmental consequences of the inconsistent application of current policies that exists between forest types is the differential regulatory process for native vegetation removal associated with vineyard development. Vineyard expansion is an increasingly important environmental issue as vineyards are expanding into upland and coastal sites, previously occupied by native vegetation (Merenlender 2000). When timberland is removed for vineyard development a timberland conversion permit (CEQA document) is required from CDF. In the North Coast wine grape growing region, CDF has approved 10 timberland conversions in Sonoma County totaling 239.9 acres, 4 in Mendocino equaling 399.5 acres, 19 in Napa for 388.44 acres; and there are 18 others pending approval. Of these, two EIRs were requested by local planning departments; which resulted in one company electing to drop their request and the other opting for withdrawal of the project following strong public concern expressed during the CEQA public review process. It is important to note that the total amount of timberland converted is often less than the area of vineyard developed.

By comparison sites not designated as timberland, such as oak woodlands and shrub communities, are not afforded protection under the Forest Practice Rules, and therefore are not given categorical statewide considerations under CEQA, thereby circumventing environmental review and public participation. As a consequence, thousands of acres of oak woodlands and rangelands have been removed to establish new vineyards throughout coastal California (Merenlender 2000) without a systematic environmental review process prior to conversion. This inconsistent application of environmental policy makes it virtually impossible to assess cumulative impacts for the proposed development and inhibits any comprehensive analysis of the environmental impacts across the landscape.

While region-wide vineyard development can have a wide array of adverse effects on forests, watersheds, wetlands, fish, and wildlife (Garrison 2000), these impacts are not likely to be adequately addressed by local oak woodland protection initiatives not subject to CEQA. Furthermore, local policies have historically been designed to conserve soil and protect water quality as a means of addressing county-based fiscal restraints. Additionally, counties often exempt agricultural development from CEQA review in response to strong vocal opposition.

The following examples illustrate how policies addressing environmental impacts of agricultural expansion have developed at the local level. In all cases, committees representing diverse interests including agriculture and environment were involved in the policy development.

1) After a large number of oak trees were removed for vineyard development in Santa Barbara County, the County began a collaborative process to address oak woodland protection that brought together people with diverse interests through a series of workshops. In November 1998 there was a narrowly defeated oak woodland protection ballot initiative in Santa Barbara County. Eventually, a set of guidelines to mitigate the environmental impacts of oak tree removal and to maintain viable oak habitats was established through the collaborative process. Subsequently, the Board of Supervisors directed the planning department to develop local regulations based on the results of the workshops that would set thresholds for oak removal depending on the parcel size and species proposed for cutting. Most recently, the Board has requested that the oak protection ordinance include an option for farmers to submit their own management plan that addresses oak conservation to a designated committee for review in lieu of the regulatory requirements.

2) Lake County has a set of voluntary vineyard and land-clearing guidelines that were established primarily to address erosion impacts on the water quality of Clear Lake. This non-binding review process applies only to conversions from existing agricultural land (continuously in agricultural production during the past ten years) to vineyard and has been implemented on a trial basis. In addition, the County has a grading ordinance that applies to clearing more than 10,000 square feet of native vegetation and is subject to review under CEQA.

In December 1999 Lake County required that a vineyard development project, which would clear 100 acres of native vegetation including blue oak (*Quercus douglasii*) and chaparral habitat, be subject to a focused EIR. A focused EIR requires that a specific subset of potential environmental impacts be analyzed rather than the more comprehensive environmental impact studies mandated for a full EIR. This was the first vineyard development that was obliged by a county to produce such a document. This decision sent shock waves through the agricultural community both locally and statewide.

3) Napa County has conservation regulations aimed at vineyard development intended to minimize physical disturbance to a site, prevent soil erosion, improve water quality, preserve riparian areas, and avoid development of steep slopes. The regulations were put into place in 1991 and require setbacks from stream corridors of 35 feet for flat areas and 105 feet and greater for slopes over 40 percent. Napa County also requires that an erosion control plan be submitted prior to vineyard planting. In September 1999 the Sierra Club filed a lawsuit against Napa County

stating that, through the erosion permitting process, the County was making discretionary decisions on erosion control plans for proposed vineyards less than 30 percent slope without applying a CEQA review. They also filed suits against some landowners who were developing vineyard on steep hillsides. The suits were settled in April 2000 and resulted in the County's confirmation that discretionary review was in place without CEQA review and agreeing to pursue studies on the application of CEQA for these cases. The Sierra Club also settled with the private parties following an agreement that vineyards on slopes greater than 50 percent and that are not yet entirely graded for planting would receive environmental review through the CEQA process.

In order to avoid CEQA review, counties and cities have restricted their review process to ministerial actions only, such as checklists of best management practices in order to verify that the requirements were met. Standardized checklists of what should and should not be done for agricultural developments to protect natural resources would be difficult to develop given the differences in site characteristics that exist across the landscape. Therefore local regulators and resource conservation districts generally argue that each site is different and requires flexibility in determining the appropriate techniques to prevent soil erosion and protect water quality, let alone to assess the cumulative environmental impacts that can result from deforestation.

4) In February 2000, Sonoma County adopted a vineyard erosion and sediment control ordinance that requires erosion control plans and minimal stream set backs (e.g., 25 feet) for new vineyard development on certain slopes, and restricts development on slopes greater than 50 percent. This ordinance does not address upland vegetation removal and other habitat conservation issues. Prior to adoption, however, the Board of Supervisors ensured that the ordinance processes would be ministerial rather than discretionary to avoid CEQA.

Summary

The current forest policies and conservation strategies for California’s forests fail to recognize the natural continuum between conifer and hardwood types. As a consequence, a dichotomy has developed between statewide and local conservation strategies that creates a double standard for environmental protection and regulatory burden to landowners. Examining the North Coast case of anadromous fish and their biological dependence on oak dominated forest landscapes illustrate the need for consistent environmental protective measures regardless of forest type. Given commonly expressed policies to move toward watershed level planning, ecosystem management, and sustainable land use practices, the differential treatment of conifers and hardwoods based on economic value should be reexamined.

Current statewide forest policy relegating all oak woodland protection to local control, while maintaining regulatory oversight of conifer-dominated forests is insufficient to protect California's ecosystems. Furthermore, it continues a trend of shifting environmental planning obligations from the state to local level (Fulton 1999) without the counties being provided with the necessary resources to adequately evaluate their programs. While local oak protection policies encouraged by the Board of Forestry may have been well intentioned it is becoming apparent that where in place, these usually provide only limited review of the potential environmental impacts that can occur when extensive amounts of native vegetation are removed. As we discuss, the existing regulatory structure neglects environmental review of many large conversions of wildland due to agricultural development and makes cumulative impact analysis impossible.

The current expectation that counties will be able to protect oak woodland ecosystems and evaluate cumulative environmental impacts due to deforestation is unrealistic given that even CDF had not been able to implement such an analysis (Dunne and others 2001). County planners are overloaded trying to assess project impacts to the environment in developed areas, and rarely have the jurisdiction, resources, or expertise to protect whole ecosystems. Even in Lake County, where extensive native vegetation removal may trigger CEQA review, the scope of review is often limited and demonstrates that a local grading ordinance may not be the best planning mechanism to address wildland conservation and cumulative impacts. The lack of local resource protection is forcing Federal Resource Agencies to step in and take actions that are often extremely unpopular with the local citizenry making meaningful dialog for conservation even more difficult.

As demands on California's forestlands increase and become more varied, using commercial timber growing potential value to set the level of state funded environmental regulation is turning out to be insufficient. In an attempt to address some of the environmental concerns regarding watershed conditions the Resources Agency has enacted the North Coast Watershed Assessment Program (NCWAP). The approach is a good first step toward developing a centralized database aimed at a better understanding of the existing conditions that may be limiting anadromous fish recovery on a watershed-wide basis. Making this information available to local interest groups and government will enhance their ability to put local land use decisions in a broader environmental perspective. However, as it stands now in the North Coast, future land use can continue to go unchecked across a large extent of our coastal watersheds not defined as timberland.

Herein lies the need for statewide conservation planning and environmental review beyond timberlands into oak woodlands in order to protect California's wildlands and associated resources such as anadromous fish. A first step might be a centralized repository of information to assess environmental impacts of proposed large-scale oak woodland removal. While limited in scope, locally based oak conservation measures should also be encouraged to protect oaks within developed areas of cities and counties. Without addressing oak woodland conservation at these two scales, the current inconsistencies in forest management and local oak policies will continue to fuel the intense debate throughout the oak regions of California as land-use increases in scope and magnitude. Perhaps a blend of State oversight to ensure our oak woodland landscapes is protected and local policies that can account for resident differences in oak distribution and land use policies could improve the environmental review process that is currently lacking. Improving our ability to address landscape level oak woodland conservation would lessen the burden on small landowners who can sometimes find themselves regulated tree by tree.

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When Oak Ordinances Fail: Unaddressed Issues of Oak Conservation[1]

Rudolph H. Light[2] and Linda E. Pedroni[2]

Abstract

The mandate by the California Board of Forestry in 1993 required each of the 41 counties which have significant oak woodlands to develop programs for the ultimate protection of this resource. As of 2001, a few counties have planned for the sustainability of their oak woodlands, but some counties may not be addressing the key components that will determine the overall future status of oak woodlands across counties and regions. Most counties and cities use the individual tree as the fundamental unit of conservation and neglect entirely the need for policies on oak woodland conservation and regeneration. They instead should regard the oak woodland as the functional unit and insist on large-scale regeneration. This paper presents some psychological reasons why the ingredients of some written plans are so inadequate that the plans have a high likelihood of failure. People tend to focus on their immediate environment while ignoring important background information and they base their planning judgments on small data sets, erroneously believing them to be representative of the larger environment. This often leads to poor policy decisions. Suggestions for reframing and broadening components of oak conservation are presented.

Introduction

Tree protection has been an important aspect for American communities for well over a century. As early as 1909, the city of Visalia undertook to preserve oak woodlands through public purchase, and by 1971, had enacted an ordinance prohibiting valley oak (*Quercus lobata*) removals without a permit (Strong and George 1990). During the 1980s the State Board of Forestry considered whether or not the State should mandate oak conservation and decided against it. In 1986 the University of California Integrated Hardwood Range Management Program (IHRMP) was created to provide research and education for the management of oak woodlands. Over the past 20 years, a lot of work has been done on technical and public policy aspects of oak woodlands (Bernhardt and Swiecki 2001, Plumb and Pillsbury 1987, Standiford 1991). In 1993 the State Board of Forestry directed the more than 40 counties which have oak woodlands to develop oak conservation plans. The suggested methods fell into three categories: ordinance, general plan process, or voluntary guidelines. Prior to the Board of Forestry directive, Bernhardt and Swiecki (1991) had compiled information on how to write ordinances for preserving trees. They recognized one of the problems was the public's tendency to save "specimen" or "heritage" trees and allow cutting of younger ones. Rossi (1990) pointed out that

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ordinances sometimes resulted in loss of trees because landowners were cutting trees just under the protected diameter size. Writing and adopting plans has proven to be a great challenge.

Scientists have long known that regeneration is one of the most important factors in the health of the forests. Nearly a century ago Sudworth (1908) and Jepson (1910) noted several oak species were not reproducing well. Griffin (1971, 1973) wrote that both blue oak (*Quercus douglasii*) and valley oak replacement rates were low, as did Callaway and D'Antonio (1991) for coast live oak (*Q. agrifolia*). While adequate oak regeneration occurs in some areas, it is generally less so in the coastal ranges and foothill areas for most species (Steinhart 1978, White 1966). In southern California seedling death due to desiccation is common (Lathrop and Osborne 1990, Pancheco 1987). Muick and Bartolome (1987) surveyed the state and found that while blue oak seedlings were present, recruitment to adulthood was sporadic. Swiecki and others (1993) found wide geographic variability of blue oak sapling recruitment and stressed that many environmental variables are responsible for recruitment outcomes. According to Bolsinger (1988), the Oregon white oak (*Q. garryana*) reproduces only moderately well and in most of its range is only lightly stocked. He mentioned also that blue oak, valley oak, Engelmann oak (*Q. engelmannii*) and coast live oak were not regenerating well. It is necessary to point out that some oak species (especially those in the subgenus *Erythrobalanus*) are regenerating well over most of their ranges. Also, it appears that some species may naturally have infrequent pulses during which all the necessary environmental conditions are met to ensure seedling and sapling survival over time so as to become mature trees. Nonetheless, the trend for oak woodlands is decreasing acreage and lowered density, and impaired regeneration is an important factor.

Causes for poor regeneration have been investigated by many authors (Adams and others 1987; Borchert and others 1989; Gordon and others 1989; Griffin 1971, 1976; McCreary 1989, 1990; Standiford and others 1991; Welker and Menke 1990). Botkin and others (1991) discussed transitional and long term impacts on forests due to global warming. Brown and Davis (1991) discussed the loss of valley oaks in Santa Barbara County due to natural causes over a 60-year period, stressing the fact that there was no replacement into the canopy. They concluded by saying, "…it appears that an active program of sapling propagation is necessary to maintain or increase the size of the valley oak populations in the region."

In the last decade there has been an extraordinary political effort to conserve oaks. Some counties acted quickly in response to the Board directive, and Standiford and Bartolome (1997) commented favorably on Tehama County. By now, most counties have at least written a needs assessment, and many, such as Santa Barbara, El Dorado and Sonoma Counties, are with assistance from the IHRMP well underway with extensive and careful conservation planning. However, in most counties tangible results by and large have not been achieved.

One can enumerate the reasons for the oak woodland losses: residential development, agriculture, woodcutting, wildfire, rangeland improvement and most recently sudden oak death. In this paper, we would like to reframe the issue of oak ordinances and regulations and their lack of success in several ways which will be unfamiliar to many. One of us is a psychologist and naturalist, and we address the issues as friendly critics seeking explanations as to why the process for effective oak woodland protection is taking so long. Our thesis is that planners and citizen groups tend to focus on the wrong things when it comes to oak woodland conservation.

Conversions from Oak Woodlands

The most crucial issues as far as policies are concerned are how counties regulate the conversion of oak woodlands to other uses, and how counties mitigate when losses of oak woodlands occur *(table 1)*. These conversions include six categories, and each will be discussed in the context of existing regulations.

Table 1—*Selected counties: highlights of mitigation policies.*[1]

Alameda-1994 general plan	General policy of requiring tree replacement
Calaveras-1996 guidelines	suggests tree replacement when removed for construction
Contra Costa-1994 ordinance	pay fees for tree removal; replace when protected tree damaged
Fresno-1997 draft guidelines	suggests tree replacement when removed for construction
Glenn-1994 guidelines	suggests landowner plan should address seedling regeneration
Lake-1995 guidelines	site specific through vineyard regulations, grading ordinance
Los Angeles-1993 ordinance	may require tree relocation or replacement with 2 for 1 with 2 years care; if not feasible pay fees into oak forest fund
Madera (Eastern)-1999 guidelines	suggests to reforest through natural or artificial regeneration
Marin-1999 ordinance	regeneration and replanting encouraged, can be required to replace trees; if not feasible pay fees into tree replacement fund
Mariposa-1995 guidelines	suggests to reforest through natural or artificial regeneration
Monterey-1997 ordinance	may require relocation or replacement at 1:1 ratio; or other requirements as needed to mitigate environmental impacts
Napa-1999 ordinance	required to replace tree on ridge line or hilltop if visible from public roadway
Nevada-2000 ordinance	removal requires inch for inch replacement with long-term maintenance; if not feasible pay fees into tree preservation fund
Placer-1996 ordinance	may require replacement in kind inch for inch, propagation, revegetation; if not feasible pay fees into tree preservation fund
Riverside-1997 ordinance	mitigation required only in case of unlawful removal; same species replanted in same spot within 6 months
San Luis Obispo-coastal zone 1995 ordinance	requires replacement when removed for development or safety
Santa Barbara-2001 proposed ordinance	requires replacement and maintenance; if not feasible pay fees into oak tree conservation fund; management plans may also be required
Santa Clara-1997 ordinance	mitigation required only in case of unlawful removal; may require replacement at 10:1 ratio
Shasta-1995 guidelines	suggests protecting seedlings on rangeland and replacing trees when removed for construction
Sonoma-1989 and 1997 ordinances	for valley oak, must plant seedlings, retain other valley oak, or pay in lieu fees; for other protected oaks, may require replacement or fees as determined by value charts
Tehama-1994 guidelines	suggests replacing trees when removed for construction
Tuolumne-1995 guidelines	suggests replacing trees when removed for construction
Yuba-1996 general plan	general policy to avoid oak tree removal and to encourage protection and regeneration; removal of valley oaks should include replacement program with maintenance and monitoring

[1] Counties without mitigation policies: Amador, Butte, Colusa, Kern, Mendocino, Merced, Stanislaus, Tulare.

Specimen Tree Trap

Counties and cities typically spend large amounts of money and time to save the heritage or landmark trees and at the same time ignore the losses in the forest. We call this the "specimen tree trap." Consider a typical ordinance, say from Santa Clara County. Trees are protected if they have a diameter of at least 12 inches at 4.5 feet above the ground, but only in certain areas of the county. In the agricultural areas, limited firewood cutting is allowed, and the larger the parcel the more cutting that can be done, so that up to 10 percent of the trees of 12 inches or greater diameter may be cut in any one year (Santa Clara County 1995, 1997). Mitigation to control erosion is required in the context of harvesting but not to mitigate the loss of oak woodland habitat. Legally, one could on larger parcels remove all protected trees in just over a decade. There is no provision for replanting trees after harvest. Nonetheless, one best not remove a specimen tree. If a heritage tree in Santa Clara County is cut, the potential fine is $200,000. In Contra Costa County, removal is limited if the diameter is 6.5 inches or greater (Contra Costa County 1994). However, the idea of saving oak woodlands is barely mentioned and not enforced. There is nothing in either of these ordinances or in the one from Marin County or in many others, about saving woodlands, but there is a great deal about saving the large and mature trees. Since some counties primarily use diameter for determining which trees to protect, as a result saplings are not protected *(table 2)*. In contrast to other counties, Marin County at least recognizes and states that it will not address the issue of lack of regeneration (Marin County 1996, 1999).

Table 2—*Selected counties: tree removal size which may require a permit.*[1,2]

Alameda-1997 general plan	20 in circumference native, 30 in circumference introduced
Contra Costa-1994 ordinance	6.5 in dbh (or groves of 4 or more trees)
Los Angeles-1993 ordinance	8 in dbh
Marin-1999 ordinance	6 in dbh (this dbh specific to oaks)
Monterey-1997 ordinance	6 in diameter 2 ft agl
Nevada-2000 ordinance	36 in dbh (specific to oaks) or hardwood grove with ≥33 pct canopy; Nevada City Area 10 in dbh
Placer-1996 ordinance	6 in dbh when >50 pct of trees removed
Riverside-1997 ordinance	6 in dbh and 15 ft high if on parcel >0.5 acre and above 5,000 ft
San Luis Obispo-coastal zone 1995 ordinance	8 in dbh
Santa Barbara-2001 proposed ordinance	4 in dbh for deciduous oaks; 8 in dbh for live oaks
Santa Clara-1997 ordinance	12 in dbh
Sonoma-1989 and 1997 ordinances	9 in dbh; valley oak has own regulations
Yuba-1996 general plan	6 in dbh specific to valley oaks

[1] Counties without diameter stipulation: Amador, Butte, Calaveras, Colusa, Fresno, Glenn, Kern, Lake, Madera (Eastern), Mariposa, Mendocino, Merced, Napa, Shasta, Stanislaus, Tehama, Tulare, Tuolumne.

[2] There are many exceptions; agricultural and rangelands are often exempt or have less stringent regulations.

The most striking example of the specimen tree trap in northern California is the Danville Oak, located in a median strip of a four-lane road. Its roots are covered with pavement. This is a valley oak, perhaps 300 years old, moderately diseased and senescent. According to the arborist, it will live for perhaps another 50 years with careful management (Peña 2000a, 2000b). The town council voted to spend $150,000 (later reduced to $70,000) to put a steel structure around this oak to protect cars and people from tree breakage. However, if one looks carefully at the outskirts of town, one realizes that the real problem for Danville's oaks rests with the development pressure in the hills to the west, where thousands of houses already exist. There is some protection through park dedication in the hills, but the citizens and planners focused their time and a lot of money on the tree and not the forest. This can never result in oak woodland preservation.

Vineyard Conversion

Vineyards are perceived by many as a major cause of oak woodland decline. However, in most places, the new vineyard impact is exaggerated. It is only one important factor in the loss of oak woodlands, and sometimes seems more important than other causes because of the high visibility of some new vineyards. As we begin this topic it is time to discuss some findings from cognitive psychology. Since this paper focuses on public policy of oaks more than psychology, we will keep psychology theory brief, merely making the connection between the two subjects. Please bear in mind that there is a body of experimental evidence regarding human behavior under consideration here, and it has been applied to political processes. Humans typically overestimate the frequency of rare events, say airline crashes and underestimate the frequency of common events, such as herpes (Lichtenstein and others 1978, Light 1983, Slovic and others 1976). The same two psychological misperceptions occur for forest land. We also tend to rely on small numbers to make our decisions (Tversky and Kahneman 1971). We focus on the immediate and visually important things which we believe impact us directly. Merely stating that humans tend to focus on the immediate is of course trivial. What is more cogent is that experimentally, humans have been found to consciously disregard and dismiss that which is not immediate even though people may be well aware there is more information than that which they use. Thus, if a phenomenon is out of sight or simply out of our neighborhood, even if we are cognizant of it we discount its importance. Hence, a rational decision about the Danville Oak was not made and the real problems for oak woodlands were ignored. In our discussions with planning staff, we found that some of the planners knew that their plans only focused on preservation of individual trees, but other planners believed that was all that was necessary. We can state that in talking to planning staff personnel of many counties, no small number are frustrated with the slow pace of oak conservation no matter how defined or delimited.

Many people would be surprised to learn how much oak woodland exists in California. Surveys using different methods and at different times yielded similar and credible results. Bolsinger (1988) estimated that there were 9.6 million acres of hardwood rangeland in California and that 72 percent of the hardwood types were in private hands. The most recent survey is that of Greenwood and others (1993), revised by Biles and Love (1998). According to them, there are 10.5 million acres of hardwood rangelands in 45 counties with about 70 percent in private ownership. Nearly three-quarters of a million acres are reserved in both private and public sectors. Many citizens would underestimate the total oak woodland acreage and overestimate the number of trees at risk.

With what we have just said in mind, three counties may be used as examples to discuss the conversion of oak woodlands to vineyards: Santa Barbara, San Luis Obispo, and Lake. The Santa Barbara story is now famous as a case study of how to develop plans for tree and oak woodland preservation but it has been a long and often ugly process. It was triggered by a perceived threat, a minor threat, the loss of fewer than 900 oaks on a single project of 500 acres of grazing land converted to grape vines. Had those oaks not been visible to passersby and had they not been *perceived* to be the last of a breed, less attention would have been given to them and the Santa Barbara story would have evolved differently, hopefully to the same end but in a much less divisive manner. In 1995 in Santa Barbara County, there were 8,976 acres of grapes, and in 2000 15,869 acres (California Agricultural Statistics Service 2001). Much of the new planting is on land that was previously devoted to grazing and did not involve clearing oak trees (Leider, personal communication). In response to this one project and fearful of more conversions to vineyards, a long public process was initiated to write an ordinance based on an environmental impact report (EIR), such report and proposed ordinance only covering lands in the private sector. The Santa Barbara County Oak Tree Protection Program EIR reports only the oak woodlands of 198,000 acres on private property in the project area, and omits entirely the oak woodlands on public lands (Santa Barbara County 2001). Looking at the big picture, Santa Barbara County has about three times the amount of oak woodland cited in the EIR, a total of 634,600 acres of hardwood rangelands (Biles and Love 1998), hardly on the verge of extinction. There are 356,000 acres under public ownership, and 278,600 acres in private hands. So this project which resulted in the removal of the oaks on the 500 acres accounted for about 0.2 percent of the privately held oak woodland, and 0.09 percent of the total oak woodland in the county. We know many of these trees on the subject property were valley oaks but their loss was still minor compared to the total. The attention paid to the few oaks which were removed is greater than rationally justified based on total hardwood rangeland acreage. It needs to be said that Santa Barbara County currently is undertaking extraordinarily comprehensive planning for oak woodlands, and it goes well beyond vineyards.

San Luis Obispo County is a little different. They have workable tree and habitat protection in place, but only in the coastal zone. As of 2000, there are 20,425 acres of vineyards, up from 10,055 acres in 1995 (California Agricultural Statistics Service 2001). New vineyards are going in with some oak displacement but most of the vineyards are being developed on pre-existing agricultural land (Trinidad, personal communication). The concern with conversion to vineyards is to some extent based on the concept of perceived acceleration of conversions as well as the total acreage. Data and projections are as yet inadequate to determine final vineyard development.

The types of woodlands in this county are highly disparate. Coast live oak and blue oak habitat are well represented (242,100 and 271,300 acres, respectively), while valley oak habitat consists of only 2,700 acres. However, it is the coastal area, home to the plentiful coast live oak west of the Santa Lucia Mountains which is regulated for tree cutting. The uncommon valley oak, located inland, is without protection and without replanting requirements when one is cut. Just knowing these figures allows us to infer that if people wanted to further protect oaks in San Luis Obispo County, the county should regulate valley oak habitat, where virtually no protection presently exists. Planners there are aware of the inconsistency.

Lake County lost an estimated 500 to 800 acres of oak woodland in the period 1997 to 1999, mostly to vineyard and some to housing (Lake County 2001). There is a strong movement to control cutting trees in some areas, but no replanting requirements despite the County Resolution on oak woodlands management (Lake County 1995). Looking at the background information which does not appear in the County planning document, Lake County has 6,828 acres of vineyard, up from 2,966 in 1995 (California Agricultural Statistics Service 2001). At the same time, it has 237,900 acres of hardwood rangelands, mostly interior live oak (*Q. wislizenii*) and California black oak (*Q. kelloggii*), with significant areas of blue oak as well, but few valley oak remain. This county focuses efforts on specimen trees or the relatively few trees in and around vineyards and subdivisions. It is a classic case of ignoring the background information in favor of the individuating information and using solely the latter on which to base the conservation planning decisions.

Having used these examples where the underlying information was ignored, where the acreage of oak woodlands is markedly underestimated and decisions were made on the basis of a very small amount of land and land use change, we want to introduce a related concept. It is called the base-rate fallacy (Bar-Hillel 1980). This refers to the process of making judgments and predictions based on specific and usually inadequate information instead of taking into account the total information available. In other words, we neglect all the background or collateral information which isn't in clear view and focus on the specific and local information even though that background information is often far more salient than the local information. In the three counties discussed, dire predictions are made on the basis of a limited sample, while the hundreds of thousands of acres of viable woodlands are neither recognized nor factored into the planning. It is critical to study the base-rates prior to drawing up the regulations.

The psychological reasons for this behavior have been studied. One finding suggests that we don't pay attention to the background information because it is abstract and remote, while we feel that the specific information is concrete and salient. The background base-rate information is ignored because people, in spite of the added collateral information, believe that the base-rate *ought* to be ignored (Bar-Hillel 1980). People believe the background information has no relevance to them, nor to the decision process for the problem at hand. Having said that, we will turn to a conversion which is as yet not well studied over the long term, one which will likely be found ecologically more important than vineyards, but to which little public attention is paid and which illustrates the point.

Conversion from Wildfire

Although conversions to agriculture and development are widely reported, aftermath of wildfire is not. There is no large body of literature specific to seral succession of oak woodlands following high intensity wildfires, but general information may be located in Biswell (1989) and Wright and Bailey (1982). Mensing (1992) noted blue oak regeneration in southern California over the last 150 years is associated with fire. Holmes (1990) and McClaran and Bartolome (1989) believe periodic low intensity fires contribute positively to enhanced oak regeneration. Allen-Diaz and Bartolome (1992) found that a prescribed low intensity underbrush and grass burn after fall rains had commenced did not much alter blue oak seedling survival compared to a no burn plot. However, an out of control high intensity summertime fire with a heavy fuel load is a different matter. We believe these large-scale wildfires in oak woodlands have significant and damaging long term as well as short-term effects to the oak forests for those species which are not naturally reproducing well. We certainly acknowledge that ecological processes span more than human lifetimes, that fire is an integral part of the California oak woodlands landscape and that fire acts simultaneously with other factors to determine forest composition outcomes. But we also maintain that the relatively common occurrences of fire leads us all to disregard the significance.

We mentioned that people tend to underestimate the frequency of common events and with that, the significance of them. Fires are frequent in California. There were fires on the Light Ranch in Mendocino County in 1992 and 1995. These fires resulted in the loss of over 800 mature oak trees, some over 300 years old, including valley oak, blue oak, Oregon white oak, California black oak, interior live oak, oracle oak (*Q.* x *moreha*) and canyon live oak (*Q. chrysolepis*). We've replanted the area with nearly 1,000 acorns from local trees but without our planting efforts it is doubtful the forest would ever return, at least not for centuries. These trees are gone as surely as if removed by a bulldozer.

Every year tens of thousands of acres burn in California, and much of this is oak woodland. In 1999, on land under California Department of Forestry and Fire Protection (CDF) jurisdiction, more than 285,000 acres burned, and in 2000, over 72,000 acres burned (CDF 2001). The largest single conversion in Mendocino County from oak woodland to other habitat was by one fire in the summer of 1987, burning 42,500 acres in Mendocino County and 10,500 acres in Lake County (Schott, personal communication), much of it blue oak woodland. This specific fire started in July and became a high intensity fire which consumed whole forests. In many acres of the burn, conversion to another habitat type occurred. The fire destruction was enormous, but being humans we don't assess its significance as skillfully as we do a conversion of 300 highly visible acres to a vineyard. All the oak woodland conversions to vineyards in the last decade over the entire state hardly approach one-half the acreage or the number of trees destroyed by this one major fire. When we factor in the number of wildfires we have in oak woodlands over a year or a decade, we can conclude that fire is more destructive to oaks than conversion to vineyards. And destruction of oak woodlands by wildfire is virtually ignored unless the land is close to urban areas. Succession will in time perhaps develop an oak woodland, but given both the limited success of natural regeneration of blue oak and the several centuries required, this conversion is important and long lasting. We know of no large-scale oak reforestation program following a wildfire. The remedy to reduce this type of conversion threat is to prevent the hot fires through proper grazing management and prescribed burning, and if wildfires occur, to give the landowners technical and financial incentives to replant and reforest. Perhaps the role of wildfire in the loss of oak woodlands needs to be addressed and policies developed. Once policies are in place, the above-mentioned management practices can become part of ordinances or general plans.

Wood Cutting

In sparsely populated rural counties, woodcutting is a major cause of the loss of oaks, primarily blue oak. About 6,000 acres per year are harvested. Data from about a decade ago indicated that in Shasta County, net addition to tree volume was significantly less than the amount harvested for firewood while in Tehama County volume was marginally increasing (Standiford and others 1996). Both counties adopted recommendations for canopy retention but the authors point out that only 10 percent of the Tehama County plots and 25 percent of the Shasta County plots actually had at least 30 percent canopy retention. Rural counties by and large have voluntary guidelines for oak woodland management rather than ordinances. This has led to a curious phenomenon, illustrated by Glenn County. Its 1994 resolution to adopt guidelines refers to the "importance of private property rights" and economic viability four times but the guidelines never refer to the need to leave stumps to sprout or to plant new trees (Glenn County 1994a, 1994b). Calaveras, Tehama, Tuolumne, Madera, Mariposa and Shasta Counties have all adopted similar guidelines. In their own way, these counties just as with the city of Danville, attempt to save the older trees and allow the younger ones to be removed, only "suggesting" to keep some of all species and sizes, but there is no requirement in any of these counties to do anything to ensure this outcome. Voluntary guidelines can only suggest, so incentives are needed. The guidelines of these counties as written are a recipe for the permanent loss of the oak woodlands. The remedies for California are simple. Harvest for sustainability (Standiford and others 1990). Encourage or require replacement seedlings and saplings by planting, or mechanical protection of naturally sprouted seedlings. Conduct woodcutting in the same manner as we do fishing. Require a minimum size instead of a maximum, and replacement along with conservation. We utilize the federal Environmental Quality Incentives Program for soil conservation and state Senate Bill 271 funds for riparian restoration. We now need to develop similar cost share programs for oak woodland restoration, perhaps along the lines of the proposed Assembly Bill 242.

Residential and Other Development

In many areas of the state and the urban fringes of all larger cities such as the ones in the Los Angeles Basin where the Engelmann oak is making its last stand, residential development is the pressing problem. In fact, according to Giusti and Tinnin (1993) the single largest threat to the state's oak woodlands is residential development. Each year 30,000 acres of hardwood rangeland are lost to residential and commercial uses (Standiford and others 1996), and there is little required in the way of mitigation. The more urban counties tend to favor ordinances, and often punitive ones at that. In so doing, they do not really encourage conservation or regeneration, but merely regulate tree cutting as they attempt to save specimen trees. In a few counties, a specified number of seedlings or acorns must be planted when trees are cut. Sonoma County generally requires between a 16:1 to 32:1 replacement ratio and protection to sapling size; Santa Barbara County proposes up to 15 seedlings or 45 acorns for each tree cut, but these regulations are rare among counties. Usually, replanting is required only as mitigation for other procedures on a case by case basis, and thus fails the woodlands. The result is a permanent loss or at best, serious fragmentation.

Sudden Oak Death

As it stands today, no county has the power to remove, treat or spray an oak or other tree or shrub infected with *Phytophthora ramorum* without the landowner's permission. The lack of county authority to deal with this threat is a glaring omission and hopefully will be rectified even as research is still being conducted. In speaking with several planners in the Bay Area, the very region where sudden oak death exists, most were not aware of the 10 host species which this fungus infects nor of the ecological significance of the disease. Fortunately, the State has recently exerted some authority in the matter (Fimrite 2001). Unfortunately, sudden oak death with rampant and uncontrollable spread may cause permanent and large-scale conversion of much of our oak woodlands.

Suggestions and Summary

The problem discussed here is that those of us who care for oaks and forests have a marked tendency to dwell on the specific trees and ignore the forest. We have a belief in the truth of small numbers (Tversky and Kahneman 1971) and we not only disregard the background information, we actually believe it is unimportant. Despite claims, many in the planning business do not look at all the information. Tehama County focuses on private property rights, Visalia on the preservation of specimen trees, and Lake County on vineyards. Unfortunately, this often leads to poor decisions. We are strongly conditioned by our local circumstances and we have a difficult time extending ourselves to see the big picture (Tversky and Kahneman 1974). In being too dependent on direct information, Slovic and others (1976) point out, "…cognitive limitations force decision makers to construct simplified models in order to deal with the world." They further state, "The experimental results indicate that people systematically violate the principles of rational decision making when judging probabilities, making predictions, or otherwise attempting to cope with probabilistic tasks." We need to consider many variables simultaneously, and man has a tough time doing this, for we rely only on the immediate information and ignore the important background data.

Typically, persons in authority decide matters intuitively, what looks good in the short term, what is specific to the immediately perceived problem; in turn they embrace procedures that are easy to explain, rationalize and defend. This strategy won't work to conserve and expand oak woodlands.

However, there are solutions to our cognitive dilemma. First, we must recognize that we are prone to these cognitive errors and then adopt a new viewpoint. We need to be aware that we are dealing with a multivariate problem, which encompasses far more than trees and conversions, and which includes the whole scope of geography and in particular natural disturbance regimes, ecological succession, and expectations on the landscape over time. The planners and interested groups must shift to a multivariate approach and learn probabilistic reasoning. Following are some suggestions.

Plant Seedlings

While there is some controversy regarding the long term efficacy (or even the need) for artificial regeneration, many papers have been written on methods to enhance seedling survival and sapling recruitment (Costello and others 1991, Costello and others 1996, Griggs and Peterson 1997, Light and Buckner 1999, McClaren 1987, McCreary 2001, Plumb and De Lasaux 1997, Roberts and Smith 1982, Schettler and Smith 1980). Our personal observations and experiments lead us to believe that some intervention (at least in the North Coast Ranges) is essential. Complete artificial regeneration by planting acorns, watering and protecting the seedlings is very successful but costly, and we have found that merely caging seedlings works reasonably well for interior live oak and black oak. However, for some species we see no alternative to a complete artificial program. We believe that artificial regeneration (or at least caging natural seedlings) should become a major part in oak woodland conservation public policy to mitigate natural and human caused woodland losses. When vineyards are established, it is an easy matter to plant, irrigate and protect seedlings from herbivores. Some counties already require replanting but due to the difficulty in propagating oaks to sapling stages, we would encourage counties to require a 50:1 ratio of replacement. This would encompass any and all conversions, whether deliberate such as woodcutting, housing developments and agriculture, or if accidental such as fire or sudden oak death. Don't prohibit cutting, but grow new forests with the help of partial funding from the public sector. Encourage and help pay for planting even when no conversion has occurred. Allow offsite mitigation. Whatever else is done, plant trees on private and public lands alike.

Estimate Probability of Conversion

The current stars in the planning world are in the counties of El Dorado (Greenwood and Saving 1999), Sonoma (Brooks and others 1999) and Santa Barbara (Santa Barbara County Planning and Development Department 2001). The first two are using GIS methods to map and determine the probable places of conversions. This method needs to be expanded and quantified so that one assigns a probability estimate to the type of conversion. In the hills of Mendocino County the likelihood of adding homes is greater than the likelihood of new vineyards, and both are far less likely than fire. In the western hills of Colusa County, the pressure appears to be from woodcutting and grazing improvement, and the likelihood of residential development or vineyards is practically zero. To estimate conversion from oak woodland to some other habitat one needs to use both direct and collateral information. Every acre needs to be assigned a probability of conversion based on all the past information of nearby lands as well as on current uses. This is a complicated multivariate problem, and to estimate these probabilities requires extensive geographic information and maps at least including zoning regulations and legal land use possibilities, census data, current land use, adjacent land use, slope, soil type, climate, proximity to urban centers and transportation. In addition, knowledge of the forest or rangeland itself including species present, age structure, fuel load, and canopy information is needed. Differential protection by species will lead to better management although most counties don't address this issue *(table 3)*. The experts also need to be able to predict where oak woodlands can flourish in places where restoration is needed.

What we suggest is that planners need to adopt a probability mode of thinking and correctly assess risk of conversion in each area of every county while at the same time recognizing that it is a dynamic and ongoing challenge. Planners and politicians, bureaucrats and regulators need to learn how to properly identify and evaluate the risks, and proactively conserve the resources. We must keep in mind that potential outcomes are not equally probable, for a steep hillside is more likely to burn than to become a vineyard, and to date the risk for sudden oak death in the San Francisco Bay area is far greater than in the Sierra foothills.

Table 3—*Selected counties: differential protection of oaks by species.*

Calaveras-1996 guidelines	suggests retaining some oaks of all sizes and species
Contra Costa-1994 ordinance	all oak species treated alike
Fresno-1997 draft guidelines	suggests retaining some oaks of all sizes and species
Lake-1995 guidelines	valley oak specifically mentioned in Upper Lake-Nice Area Plan
Los Angeles-1993 ordinance	all oak species treated alike
Madera (Eastern)-1999 guidelines	suggests retaining some oaks of all sizes and species
Marin-1999 ordinance	all oak species treated alike
Mariposa-1995 guidelines	suggests retaining some oaks of all sizes and species
Monterey-1997 ordinance	all oak species treated alike
Nevada-2000 ordinance	emphasis on protecting blue oak and valley oak
Santa Barbara-2001 proposed ordinance	differentiates deciduous oaks from live oaks
Santa Clara-1997 ordinance	California black oak receives special treatment when found growing with commercial species
Shasta-1995 guidelines	suggests retaining some oaks of all sizes and species
Sonoma-1989 and 1997 ordinances	valley oak has own regulations; all other oak species treated alike
Tehama-1994 guidelines	suggests retaining some oaks of all sizes and species
Tuolumne-1995 guidelines	suggests retaining some oaks of all sizes and species
Yuba-1996 general plan	differentiates valley oak from foothill oak woodlands

Reserve Oaks on Public Lands

Biles and Love (1998) have calculated for each species the number of protected acres (private and public) it would take in each county to reach the statewide average of protected acres. For most counties, the greatest impact for the conservation of the oak woodlands could come by merely reserving oaks on the public lands. Think of the positive impact in Santa Barbara County if the planners could work with other agencies to reserve forever the 356,000 acres in the Los Padres National Forest and other federal holdings. Instead, they focused on the smaller total acreage in the private sector. Planning departments are either loath to be involved with or not knowledgeable about public lands. Many ordinances, e.g. Santa Barbara and Riverside, specifically exempt federal, state and local public lands from the regulations, although the natural resources know no boundary. Other ordinances ignore public lands altogether. Very few counties, e.g. Santa Clara, apply their regulations to public property.

Planners will say they have no jurisdiction over federal and state lands. When asked if they think these lands ought to be in the reserves, they will reiterate their position and then say they feel the private sector needs regulating. It may be naive but this sounds like a turf issue. But most planners simply do not know how much federal and state land exists in their own counties. One planner we spoke with thought her county had at most a couple of thousand acres of hardwood rangeland when in fact it is twenty times as much. Even if they are aware of public holdings, these holdings are excluded from county hardwood acreage totals leading to an underestimation and misrepresentation of the extent of total oak woodlands. Once more, we see the belief in small numbers and the underestimation of common events. By reserving oaks on public lands and planting seedlings, it would show a societal commitment to the importance of oak woodlands.

Use Existing Knowledge

In the preparation of this paper, we were struck by how many different rules there are, and with few exceptions how seemingly little communication there is among counties. There is a vast amount of information available, from state and university surveys of species by county, to ordinances and general plans available for the asking, to existing GIS studies on a variety of topics. Generally speaking, the planning documents are singular and do not benefit from the current and useful literature. While uniform regulations throughout the state may not be beneficial, at least a working familiarity with the regulations and guidelines from other counties is a necessity for everyone involved in the management of oak woodlands.

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Oak Woodland Economics: A Contingent Valuation of Conversion Alternatives[1]

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Abstract

Decisions on how much land should be devoted to oak woodland preservation is ultimately determined by society's valuation of its benefits and relative scarcity. Scarcity value can be measured by people's willingness-to-pay (WTP) to prevent oak woodland conversion to higher value land uses. In this study, we used the contingent valuation (CV) method to estimate WTP for oak woodland preservation in San Luis Obispo County (over 700,000 acres). Estimates ranged between $75 and $83 per voter, providing only about $12 million for land or easement purchases.

Introduction

Oak woodlands are found on practically all land uses in San Luis Obispo (SLO) County and represent a key part of the natural aesthetic for which the County is known. Pressures from land use conversion are diminishing and fragmenting their range. The recent growth of the wine industry brought about a rapid use conversion of specific sites within the agricultural (ag) zoning from rangeland to vineyards resulting in numerous, highly publicized oak removals. A County oak ordinance passed a few years ago only requires replacement of oaks removed on rural lands, but it is poorly enforced.

Concerns over oak woodlands have also been integrated into the larger movement to stop urban sprawl. In 1995, the city of San Luis Obispo established an open space element in its general plan to create a "ring" around the city, but a bond measure to fund purchases of these lands failed. In 2000, a ballot measure ("Save Open Space and Agricultural Resources"), patterned after similar measures in Napa and Ventura counties designed to freeze zoning, also failed to pass with 66 percent opposed.

These failed efforts to implement policies to preserve the natural aesthetic oak woodlands suggest a gap between the perception of the problems and reality of the costs of proposed intervention. The perception of many activists is that growth pressures will inevitably destroy the natural beauty of the County. But most of the voting public may not perceive this to be a problem (Rowlands 2001). In economic terms, one would say that the scarcity value of oak woodlands has not risen high enough to overcome uncertainties and compete with other uses. From a public policy

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[1] An abbreviated version of this paper was presented at the Fifth Symposium on Oak Woodlands: Oaks in California's Changing Landscape, October 22-25, 2001, San Diego, California.

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perspective, another question is "will the expected losses be irreversible by the time these environmental values become economically competitive?"

Background and Objectives

In this study, we sought to estimate the monetary value county residents would place on preserving amenity values provided by oak woodlands and other extensive agricultural land uses. We agricultural practices are most extensive, i.e., rangeland since cattle grazing is compatible with oak woodland vegetation. We further hypothesize that these land uses have two alternatives: (1) intensive agriculture (e.g., row crops), or (2) residential-commercial. We attempt to estimate the willingness-to-pay (WTP) value that would prevent three types of land use changes:

1. Extensive agricultural land use (state 1) converting to intensive, agriculture (state 2),
2. Extensive agricultural land use (state 1) converting to residential/commercial (state 3),
3. Intensive agricultural land use (state 2) converting to residential/commercial (state 3).

To emphasize the conversion pressures, a report by Standiford (1999) cited land values per acre on the Central Coast at $300-$500, $8,000, and $20,000 for states 1, 2 and 3, respectively. The WTP results address the question whether the public is willing-to-pay landowners in order to compensate them from forgoing other profitable conversions.

In an opinion poll sponsored by the California Oak Foundation (Fairbank and others 2000), 77 percent of California voters indicated their willingness for the State to use tax dollars to protect oak woodlands. However, no dollar amounts were mentioned. These conversion compensation values cannot be estimated through traditional means using market data. Even if there were a sufficient number of market transactions of each type, this would not reveal society's tastes and preferences for the environmental values of oak woodlands, just the cases where public compensation exceeds commercial values.

Currently, the only tangible expression of these environmental values comes in the form of policy and regulation to preserve these values from being lost to commercial uses. Even with perfect policy instruments, these constraints represent only the opportunity costs and not the social optimal allocation. Because policy is not perfect, land use allocations may be grossly over- or under-constrained to satisfy people's preferences for environmental values such as provided by oak woodland.

Methods

We used the contingent valuation (CV) method to estimate on these "non-market" oak woodland conservation values. Contingent valuation has been a controversial empirical tool since it does not identify revealed preferences that are known to be consistent with utility theory (Mitchell and Carson 1993). In other words, one is asking a person what they would be hypothetically willing-to-pay for something rather than observing their behavior. Nonetheless, CV has become the most popular method for such studies, due in part to recent advances in the theory and especially the testing methodology (Hanneman and Kanninen 1996, Stevens 1997, Rubin 1987) and its cost advantage over other methods.

The CV technique is best expressed by starting with the indirect utility function:

$V = V(p, q, y, X, \varepsilon)$,

where q = non-market good/service
p = price vector of market goods
y = individual's income
X = a vector of socio-demographic characteristics
ε = stochastic component of consumer's utility.

The value of q can be estimated by first offering the consumer the possibility of an improvement in their utility with a Δq such that $V(p, q^1, y, X, \varepsilon) \geq (V(p, q^o, y, X, \varepsilon)$. The probability of the consumer's willingness-to-pay (WTP) to increase their consumption from q^o to q^1 can be estimated by observing their reaction to a bid amount (A) that must hypothetically be paid:

$$P\{\text{response is “yes”}\} = P\{V(p, q^1, y, X, \varepsilon) \geq (V(p, q^o, y, X, \varepsilon)\}$$

A potentially more accurate CV method is to use a double-bound bid scheme. In the double-bound CV version, the consumer is first asked if they would pay a specific amount, say $100 (A), followed by a second offering, the amount of which depends upon their response to A (Hanemann and Kanninen 1996). If the response is “yes” to A then they are offered a larger value, A_u, or if “no” they are offered a smaller, A_l. Two or even three separate samples of a given size are obtained with each sample's double-bound bid structure different than the first in order to “map out” the probability (cumulative density function, cdf) of paying higher and higher amounts for the non-market resource. These “yes - no” response probabilities can then be converted to mean WTP estimates using a variety of statistical models.

Bid and Sample Design

The empirical approach to estimating the WTP involves

- Designing the double-bound bids (A, A_l, A_u),
- Designing the survey instrument,
- Determination of the number of sample consumers and their location
- The method for applying the instrument to sample consumers.

CV sample data collection requires a carefully designed survey instrument. Survey instrument design has a long tradition in many forms of social science research. The instrument consisted of three basic parts:

1. An introduction to the topic, designed to avoid leading the respondent,
2. A visual presentation of the three state changes for which respondents were asked their WTP to prevent the change from occurring, and

3. A set of questions eliciting information on the respondent's socio-economic and demographic characteristics (e.g., traditional ones like gender, age, income, education as well as political party, family size, renter or owner, lot size).

Images of the three states were provided so that the respondent had a reference during the survey. Example images used in the survey that characterize each state are present below *(figs.s 1-3)*.

To first learn about the WTP distribution, we conducted a pre-test involving open-ended CV questions (n=50) in order to set A to what seemed to be the median WTP. Hanneman's double-bound method requires dividing the sample into two or more sub-samples wherein different bid amounts are offered in order to adequately map the WTP cdf. Sample observations were collected for the double-bounded bid along with a set of socioeconomic characteristics using personal intercepts during the summer 1997. The County was stratified into three regions to obtain a well-distributed coverage (North County, North Coast, South County). Each survey took approximately 5 minutes to complete. Most surveys took place at the entrance to grocery stores or large retail outlet stores.

Figure 1—Typical state 1 image.

Figure 2—Typical state 2 image.

Figure 3—Typical state 3 image

Optimal specification of the bids calls for the initial bid to be the supposed median value and follow-up bids are symmetrically placed around it to “bound” 50 percent to 75 percent of the observations (Hanemann and Kanninen 1996). Since the median value is not known a priori, it is suggested that a recursive approach be used to alter the initial bid. Also, it is important to define the method of payment so that the bid offerings are realistic and relevant to the respondent. We represented the bid as a one-time payment, not an annual increase in taxes. This was done to avoid confusing the respondent and the issue.

The Phase I sub-sample median bid was $100 (A), and A_l and A_u were set to $50 and $200 (50 percent quantiles). Observing the distribution of responses in Phase I, the Phase II median bid was increased to $150, retaining the 50 percent quantiles for the follow-up offerings. Each respondent was asked to provide a "yes" or "no" response to the bid scheme for each state change permutation (1 to 2, 1 to 3, or 2 to 3). After which they were asked to provide information on their socioeconomic characteristics *(table 1)*. The upper bound for state change 1 to 3 was set at $500 in phase 1 and $750 in phase 2 in response to evidence from the pilot study that there was a willingness-to-pay much higher amounts than the other state changes.

Table 1—*Survey bid structure and socioeconomic variable.*

Sample sizes and bid amounts offered were as follows:				
Bids	n	A_l	A	A_u
Phase 1	150	$50	$100	$200
Phase 2	151	$75	$150	$300

The demographic variables included:	
X Variable	Description
EDUC	1 = grades 0-8, 2 = 9-11, 3 = 12, 4 = 12 + some e college, 5 = college degree, 6 = post-grad. degree
GENDER	1= male, 2 = female
INCOME	1 = <$10,000, 2 = $10K-$20K, 3 = $20K-$30K, 4 = $30K-$40K, 5 = $40K-$50K, 6 = $50K-$60K, 7 = $60K-$70K, 8 = $70K-$80K, 9 = $80K-$90K, 10 = $100K +
MARRIED	1 = "yes", 2 = "no"
AGE	years
RENTOWN	1 = own, 2 = rent
PARTY	1= Republican, 2 = Democrat, 3 = Independent, 4 = Other

Results and WTP Estimates

Table 2 presents the responses to the double-bound bid offerings for each state change scenario by sub-sample phase. It is clear that a majority of county residents are willing-to-pay some positive value to prevent conversion under all three scenarios. Nevertheless, the question at the center of this study is whether that amount is sufficient to be effective. *Table 3* presents the logistic regression estimates for the three state-change scenarios. All three state change models fit quite well with the bid variables highly significant along with broad significance across the independent variable set. The most practical expression of overall model fit is the "percent of sample observations correctly classified," about 90 percent in all three cases.

Table 2—*Response percentages for double-bound offerings by sub-sample for the three state change scenarios.*

State Change Phase	no-no (percent)	no-yes (percent)	yes-no (percent)	yes-yes (percent)
Extensive to Intensive Ag. (1 → 2)				
1	39.6	12.1	28.8	19.5
2	51.7	6.6	23.2	18.5
Intensive to Resid./Comm. (2 → 3)				
1	36.9	9.4	24.8	28.9
2	32.5	4.0	28.5	35.1
Extensive to Resid./Comm. (1 → 3)				
1	27.5	10.8	40.9	20.8
2	31.1	4.6	39.7	24.5

Table 3—*Logistic regression estimates for the three state-change scenarios.*[1]

	State change 1 to 2		State change 1 to 3		State change 2 to 3	
Variable	β (s.e.)	Wald stat. (sig)	β (s.e.)	Wald stat. (sig)	β (s.e.)	Wald stat. (sig)
BID	.0738 (.0106)	48.5202 (.0000)	.0899 (.0134)	45.2535 (.0000)	.0841 (.0136)	38.2593 (.0000)
EDUC	0.243 (.1946)	.0156 (.9007)	–.1073 (.2323)	.21342 (.6442)	–.2218 (.2592)	.7320 (.3922)
REPUB	.6350 (.3821)	2.7621 (.0965)	1.4808 (.4817)	9.4497 (.0021)	1.1259 (.4851)	5.3859 (.0203)
AGE	–.0400 (.0133)	9.0713 (.0026)	–.0509 (.0158)	10.3812 (.0013)	–.0380 (.0163)	5.4593 (.0195)
GENDER	–.0465 (.3632)	.0164 (.8982)	.6977 (.4292)	2.6424 (.1040)	1.0686 (.4487)	4.6725 (.0172)
INCOME	–.0056 (.0750)	.0056 (.9405)	–.0574 (.0866)	.4389 (.5077)	.0794 (.0858)	.8561 (.3548)
constant	–4.7212 (1.3032)	13.1254 (.0003)	–5.4611 (1.5621)	12.2221 (.0005)	–6.6875 (1.6259)	16.9182 (.0000)
Goodness-of-Fit	243.525		164.2		174.885	
$\chi 2$	205.975		209.338		242.686	
Pct Correctly Classified	87.59		90.34		91.03	
df	290		290		290	

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[1] The signs of the logistic coefficients have the opposite interpretation (P_{yy} {response is "yes" to A, "yes" to A_u} = 1 - $F_c(A_u; \beta, \theta)$). The standard t-test can be used by replacing the standard error of the estimate with the asymptotic standard error. The Wald test is used in this case, which is the square of the t-value.

State Change WTP Estimates

The practical end of these results is to reduce this empirical information to a single "summary" measure (1st moment) of WTP. Two summary statistics, the mean and median, have been debated at length in the CV literature (Jakobsson and Dragon 1996). Although much can be made of the theoretical differences in the two measures, they are practically the same value, at least in this study.

The mean WTPs for each state change are as follows (*fig. 4* illustrates the cdf's by state change):

1. Extensive ag. lands (state 1) to intensive ag (state 2) = $83
2. Extensive ag lands (state 1) to residential/commercial (state 3) = $75
3. Intensive ag lands (state 2) to residential/commercial (state 3) = $80.

Lacking a statistical analysis of these differences, little should be made of any perceived differences, despite the apparent lower valuation of converting extensive ag lands to residential/commercial than the other state change scenarios. Comparing the distribution of responses to the mean WTPs reveals the importance of the mean calculation *(table 3)*. Though a bond measure focused on oak woodland preservation would have the highest likelihood of passing, the borrowed funds at issue could not be very large in order for the measure to pass. In any case, the low magnitude of all three WTPs becomes the main issue.

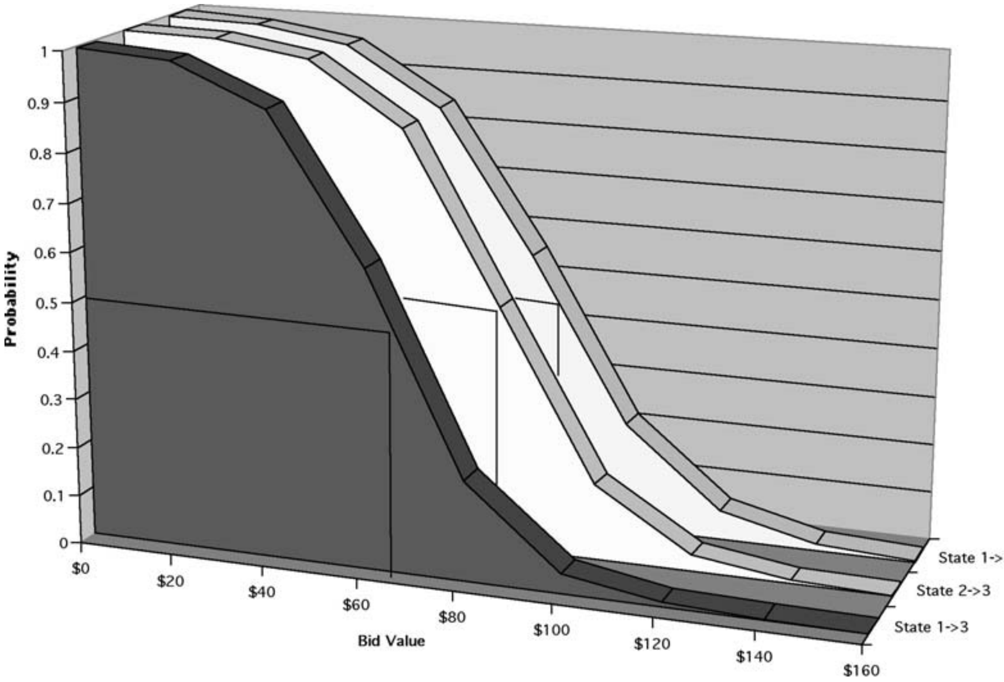

Figure 4—Cumulative density functions for each state change, showing median WTP estimates.

Summary and Conclusions

A number of preliminary conclusions can be drawn from the results. While a majority of residents did express a willingness-to-pay to prevent the conversion of oak woodlands, they also expressed a positive willingness to prevent the conversion of intensive agricultural lands to residential land use. Clearly, any voter financed fund for conservation easements could not be limited only to oak woodlands. The bid value associated with preventing the conversion of oak woodlands was lower than the two other conversion scenarios.

Again, these are hypothetical one-time payments. Multiplying these values by the county voters (142,000) could conceivably provide about $12 million for the purchase of lands or conservation easements. If a bond measure were passed, the available funding would generate only a small fraction of the funds needed. With nearly half million acres of woodlands at risk, only a few key properties could be selected for protection. Any attempt to preserve the much more costly intensive ag lands would quickly consume the funds. With values running around $20,000 per acre for lands under pressure for development, only 600 acres could be purchased.

These WTP estimates reflect a low level of tangible concern over oak woodland protection in SLO County. To explain the underlying reasons for such complacency is the subject of another study. Nevertheless, it could be that since urban sprawl has not reached the level of counties like Napa and Ventura, voters are less worried about threats to the County's aesthetic character. Intensive agricultural may also be viewed as a barrier to sprawl. Finally, the combination of steep topography and National Forest ownership within the viewshed of most SLO communities may be considered as making it unnecessary to pay for more protection against land use conversion.

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Working Woodlands: Public Demand, Owner Management, and Government Intervention in Conserving Mediterranean Ranches and Dehesas[1]

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Abstract

The contributions of California and Spanish oak woodlands to owners, neighbors, and society are undervalued. Recent Spanish studies have begun to identify the components of value provided by traditional oak woodland agro-sylvo-pastoral systems, including environmental and self-consumption values. Work in California has revealed that self-consumption by owners, benefits to neighboring properties, and benefits to the larger society are important components of the total valuation of traditional low-intensity oak woodland ranching. In Spain, this type of bioeconomic analysis, known as "Total Economic Value," engages an institutional framework at pan-European, national, and regional levels as the full economic values of low-intensity agriculture are increasingly recognized and supported by subsidies and public policy initiatives. In California oak woodlands this accounting helps provide a means for assessing conservation investments by third party non-governmental organizations, and sheds light on oak woodland landowner behaviors crucial to efforts to conserve these mostly private lands. We embark on a course of research to conduct comparative bioeconomic analysis in Spain and California, including evaluation of the ecological outcomes of various scenarios, and the institutional leverage points for such information. This paper introduces ecological, economic, and institutional similarities and differences in the woodlands, with particular attention to the possibilities of comparative bioeconomic analyses.

Introduction

The undervaluing of traditional oak woodland agro-sylvo-pastoral systems in California and Spain has resulted in misguided government policies and interventions, and misunderstandings of landowner goals and behaviors. We are embarking on a collaborative, multi-disciplinary project of comparative bioeconomic analysis on privately managed oak woodlands, with the goal of developing strategies

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that will increase the contribution of oak woodland ranches in California and Spain to conservation and quality of life locally, regionally, and at larger scales. In Spain, "Total Economic Valuation" of oak woodland ranches has engaged policy initiatives at regional, national, and pan-European levels. In California, the fit of this type of bioeconomic information with current institutional structures is less clear. We argue that a "total valuation" analysis in California will help elaborate the value of non-governmental organization investment in oak woodland conservation, an increasingly important factor. It will also lend fuller explanation to landowner behavior and stewardship incentives, and help locate and explain opportunities and weaknesses in oak woodland conservation policy and practice.

However similar the flora and the climate, and the way they look, Spanish and Californian woodlands have quite different ecological dynamics and institutional settings. This affects the environmental consequences of shifts in economic valuation and land use, and means there are different institutional leverage points for bioeconomic information. First we describe the settings: the characteristics, ecology, and management of the two oak woodlands. Then we discuss valuation methods as applied in each setting. We conclude with a few words about institutional capacity to respond to problems, and future work.

The Woodlands

When the Spanish settled California late in the eighteenth century they found a familiar countryside of grassland and open oak woodland and savanna. Annual rainfall ranges from about 200 mm to more than 1,000 mm, but is most notable for its high variability and summer absence. The Mediterranean climate of both areas means winters are cool but freezes are rare.

In some ways the oak woodlands and savannas of Spain and California were more different in 1769 then they are today. Prior to Spanish colonization perennial bunchgrasses were a major component of California grasslands. Today these are scattered amid a matrix of hundreds of species of annual grasses from all over the world, including Spain. Wild oats (*Avena* spp.) and numerous other annual species are widespread in both woodlands. In the eighteenth century, California was home to an indigenous population of several hundred thousand. Native Californians have a history of thousands of years of oak woodland management that was undermined and ignored by California's post-Columbian society. Spain over the last several hundred years has been a land of conquest and reconquest, with successive kingdoms and influxes of peoples from the north and south. Yet the evolution of rural practices for oak woodland management progressed until the extent of oak savanna peaked early in the twentieth century (Campos-Palacín 1997).

In Spain two evergreen oak species are common in the open woodland-savanna formation characteristic of the west and southwestern Iberian peninsula *(fig. 1)*. Holm oak or encina (*Quercus ilex* and/or *rotundifolia* or ssp. *rotundifolia* or *ballota*) is most widespread and grows throughout Spain. Cork oak or alcornoque (*Q. suber*), is found intermixed with holm oak when soil conditions and location permit, preferring siliceous soils and moister conditions. There are several deciduous species that are also common in some areas, one is quejigo, *Q. faginea,* found at elevations of 600 to 1,200 m. including on calcareous soils, and another is mellojo, *Q. pyrenaica*, similar to California's black oak found at elevations ranging from 400 to 1,600 m, though sometimes as high as 2,100 m, growing best on siliceous soils (Real Jardín Botánico de Alcalá de Henares 2001). In about 45 percecnt of wooded dehesa, Holm oak is found alone, cork oak is found alone in 5 percecnt, and 50 percecnt is a mix of any of the major four and sometimes other oaks (Joffre and others 1988). About half of the wooded dehesa is found in the region of Extremadura, where 65 percent of cork oaks are found growing together with holm oak, 31 percent are in pure stands, 2.4 percent grow with mellojo, and 0.2 percent with quejigo. Nearly half has a grassland understory, almost a third a shrub (mattoral) understory, 14 percent is cultivated, and the remaining area is patchy (Cardillo 2000). Savanna formations are most common at 400 to 800 m above sea level on poor, acidic soils.

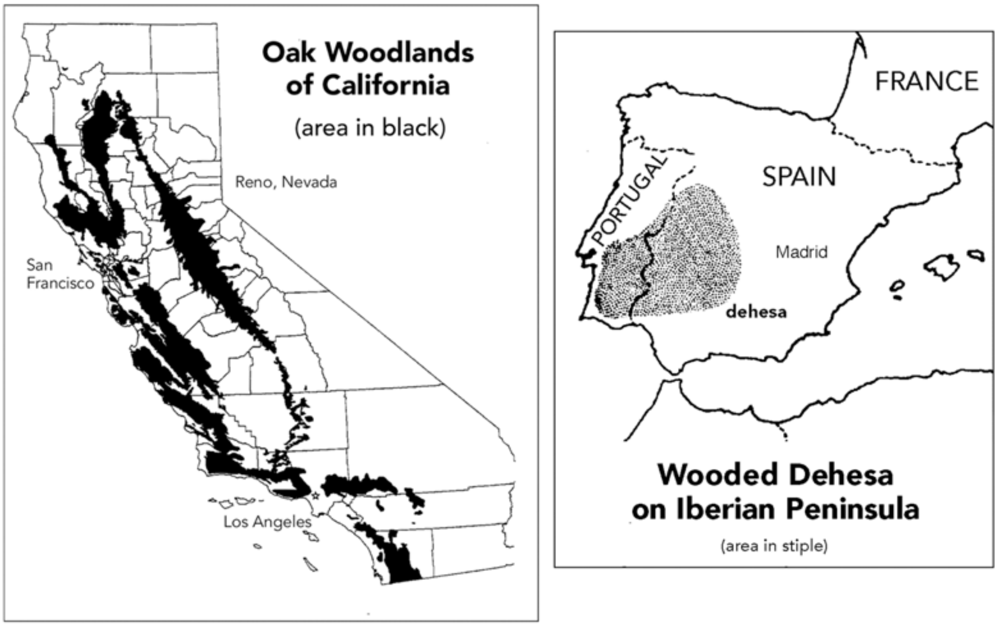

Figure 1—Californian oak woodlands and Spanish dehesa.

Californian oak savanna has four oaks that are considered particularly widespread and characteristic: the deciduous blue (*Q. douglasii*), and valley oaks (*Q. lobata*), and the evergreen coast live (*Q. agrifolia*), and interior live oaks (*Q. wislizenii*). Savanna generally occurs at elevations ranging from 60 to 700 m on a wide variety of soils, and includes communities dominated by each of the four species, as well as mixtures of these species. More than 85 percent of understories are dominated by annual grasses, with the remainder having shrub understories. By far the most common savanna types are those that include blue oak (Allen-Diaz and others 1999). Englemann oak, *Q. engelmannii*, is common in parts of southern California, and Oregon white oak, *Q. garryana*, in the north, but distributions are relatively small.

More than 300 vertebrate species inhabit California's oak woodlands and savannas (Jensen and others 1990), and it is perhaps the most significant wildlife habitat in the state on a regional scale. In Spain, dehesas support a number of Spain's endangered species and Europe's migratory birds (Diaz and others 1999). Dehesas have qualified as habitats to be preserved within the European Union Habitats Directive because of their high biological diversity. Unique breeds of Spanish cattle are also found only in the dehesa. Public interest in open space, recreation, and purchasing large recreational or “amenity” properties has increased steadily over the last 25 years, adding considerable value to Spanish and Californian oak savanna. In each country, there is widespread concern about the stewardship, regeneration, and extent of oak woodlands. The importance of each as a priority for conservation efforts varies locally and regionally.

Management

Management practices and ecological dynamics characteristic of Spanish and Californian oak savanna differ. A decline in landowner investment in Californian oak woodland may result in gradual or no vegetation change, depending on site characteristics. In Spain, substantial investment is required to prevent rapid change that results in the disappearance of open woodland within twenty years.

Spanish savanna is a human-engineered agroecosystem developed over hundreds of years known as “wooded dehesa.” Without management, dehesas become a tangle of brush and oaks. The shrub layer in a dehesa is suppressed to produce a grazable understory. Oaks are spaced as close as 8-10 meters apart in all directions *(fig. 2)*. It has been suggested that at the southern, drier extent of the dehesas, tree spacing is strongly influenced by annual rainfall and fewer than 10 oaks/ha may be found. At the north end, the limit to tree density seems to be maintaining understory productivity (Joffre and others 1999). The ideal is between 30 and 60 oaks per ha, with an average of 45. Commonly, tree canopy cover is 40-60 percent.

Figure 2—Oaks are evenly spaced in southwestern Spain’s wooded dehesa.

Trees are pruned to produce acorns and open the canopy. With a 40 percent oak canopy cover, 96 percent of the soil surface is still grass covered (Hernandez 2001). To maintain the open understory, many dehesas must be disked every 3-10 years, otherwise the understory is invaded by unpalatable shrubs, such as rockrose species (*Cystis* spp.), referred to as "jara." The dehesa is typically grazed to a golf course-like appearance by late summer. Paleoecological study suggests origins for the modern oak dehesa as early as around 500 B.C., and an earlier prehistoric dehesa with origins as far back as 4000 B.C. (Joffre and others 1999).

In California, savanna oaks are bunched in the swales, or rocky areas, or are irregularly scattered. Controls are seed and seedling predation, shade, drought, fire, and microclimate. Over much of its extent, the savanna is stable for decades, with irregular, limited regeneration and little shrub invasion. Research has shown great variability in overstory effects, both within and between years. In higher rainfall areas, canopy cover suppresses understory forage production, but in low rainfall areas, may enhance it (Allen-Diaz and others 1999). Oak woodland landowners with oak canopy covers of less than 50 percent were significantly less likely to cut oaks to increase forage production in a 1985 statewide survey (Huntsinger and others 1997). The widely recommended grazing management practice in California is to leave several hundred kilograms per ha of ungrazed grass behind at the end of the season.

The savannas in each realm are mainly used for dryland grazing *(table 1)*. Livestock producers own 56 percent of Californian oak woodlands, but livestock graze more than 70 percent (Huntsinger and others 1997), using land in public, utility, speculative, or amenity ownership. In a recent study of ranchers in the fast growing Central Sierra, almost all the ranchers studied leased land to augment private holdings (Sulak and Huntsinger 2002). The California ewe herd has decreased from 620,000 to 330,000 head in the last 10 years, while beef cows declined from 955,000 to 800,000 (California Agricultural Statistics 1990-2001). Calves are the major source of income, trailed by firewood, game, and lamb.

Wooded dehesas are most common in the regions of Extremadura, western Andalucia, and Castilla y Leon. Each type of dehesa, comprised of one or more oak species, has peculiarities of management and use. The traditional, diversified dehesa system is capable of producing a sizable assortment of commercial products *(table 1)*. It is not unusual to see cattle, horses, goats, and sheep grazing together or sequentially on the dehesa. In the fall months, pigs are grazed in many woodlands, producing a particularly costly acorn-fed ham known as jamon serrano (Parsons 1962). Income from the renting out of land for organized hunts is also common, for which there is new-found ardor in the post-Franco era as a kind of conspicuous consumption.

Transhumance, a summer migration to higher-elevation range, was once common practice in California and Spain, but has declined as stock migration routes are closed off by development and land use change, and higher elevation lands are set aside as parks and preserves. The shift to cattle, and the failure to take them elsewhere in the summer, has changed grazing patterns.

Regeneration of oaks is of concern in both Spain and California. Recruitment has been characterized as sparse to absent in California's coast live oak, blue oak, and valley oak woodlands and savanna (Bolsinger 1988), but there is considerable site to site and study to study variation (McCreary 2001). There is growing concern that for a number of reasons, including changes in grazing, fire frequencies, grassland species, shrub distribution, hydrology, and wildlife population dynamics, the natural regeneration that once sustained the woodlands is inadequate.

Table 1—*Spanish wooded dehesa and Californian savanna.*

	Californian savanna	**Spanish wooded dehesa**
Extent	3.8 m ha savanna out of 7.4 m ha total oak woodlands and grasslands (Allen-Diaz and others 2000).	2.2 oak woodland dehesa out of 6 m ha dehesa woodlands, shrublands, and grasslands (Díaz, Campos-Palacín, and Pullido 1997).
Most common oak	Blue oak (*Q. douglasii*)	Holm oak (*Q. ilex*)
Ownership	80 pct + private (Ewing and others 1988) 56 pct owned by livestock producers (Huntsinger and others 1996), much is leased (Sulak and Huntsinger 2002).	75-80 pct+ private based on study of a representative area in Extremadura (Campos-Palacín 1996) 100 pct are livestock producers.
Average ranch size	800-960 ha (Huntsinger, Buttolph, and Hopkinson 1997; Sulak and Huntsinger 2002).	670 ha (Campos-Palacín 1996)
Amenity & investment ownership	Increasing owner self-consumption of environmental services	Increasing owner self-consumption of environmental services
Land use	70 pct of woodlands are grazed (Huntsinger, Buttolph, and Hopkinson 1997).	Agro-sylvo-pastoral complex, “Dehesa”
Stocking rate of livestock (does not include wild herbivores, nor does it meet total animal demand)	5-10 ha/A.U./year (Ewing and others 1988).	4 ha/A.U./year in Extremadura (Campos-Palacín 1997)
Small stock	Declining	Declining
Large stock	Declining; 92 pct of animal demand is cattle (California Agricultural Statistics 1990-2001)	Increasing; 42 pct of animal demand is cattle (Campos-Palacín 1997).
Commodity products in use	Beef, lamb, wool, firewood, game, grazing resources.	Beef, Iberian pig, lamb, acorns, firewood, hay, cereal grain, grazing resources, wool, cabrito, goat milk, game, trufa, charcoal, cheese, fodder, honey, cork.

Spanish researchers have found that without direct efforts at oak regeneration, predictive models based on assessment of existing stand structures indicate that nearly eighty percent of the dehesa will eventually become treeless (Martin 2001). This is generally attributed to changes in grazing patterns and high stocking rates, coupled with a lack of landowner attention to regeneration.

In the last 3 years, concern has grown about oak mortality in California from a phytophthora fungus known as "sudden oak death" syndrome. A reduction of tree densities due to the death of Spanish holm and cork oaks from a similar ailment, referred to as "seca," has also been noted. Seca is not fully understood, but has been attributed to incorrect pruning, old age, plowing too close to trees and other factors related to soils and site characteristics (Diaz and others 1997).

Declining Woodland Extent

At the close of the 1950s rural Spain was in financial crisis. Prices for dehesa goods like ham and charcoal fell, pig diseases increased, much of the rural population emigrated to urban areas, and changes in cropping practices led to the collapse of the existing transhumance. The Spanish government tried to increase the value of rural production by subsidizing a shift to improved cattle cross-bred with foreign breeds, and to cereal production. The newer livestock breeds required more feed, raising demand for pasture and crop fodder. Increased dependency on concentrate and outside forage resulted in artificially high stocking rates that halted oak recruitment in many areas. The quality of grazing land decreased, trees and regeneration were neglected, and shrubs were allowed to invade from the surrounding brushlands or matorrales. Government-sponsored afforestation plantings with eucalyptus and pines covered vast acreages, many of which have deteriorated since from pathogens, wildfire, and arson. Subsidies were provided for pulling up holm oak, cork oak, and wild olive until the early 1970s. Changes in ownership laws and high prices for game hunting caused many farms to convert to hunting enterprises. Game fences are put up and the shrub layer is allowed to return. Encouraging intensification of agriculture was justified by high crop prices, including a protected cereal market, minimum levels of public recreation at the time, and inattention to the long term depletion of natural capital in trees and soil. A resulting decrease in the dehesa area has been noted by researchers (Diaz and others 1997). Fortunately this push has been countered in recent years.

Livestock grazing in California's oak woodlands began along the coast in 1769, becoming widespread with the 1849 gold rush. Agricultural conversion, firewood harvest, and development for housing have reduced the extent of the oak woodlands by about half since the 1800s (Burcham 1957). In recent years, conversion of woodlands to housing and vineyards has been increasing at an exponential rate (Huntsinger and Hopkinson 1996). In the 1940s through 1960s, state and federal programs subsidized the removal of oaks for increased forage production, in an era characterized by the drive to increase commodity production and inattention to the environmental costs.

Valuing Oak Woodlands

There is increasing recognition of the value of oak woodlands in Spain and California. Numerous studies of the likely behavior of landowners with regard to land conversion, tree harvest, and wildlife habitat retention have been conducted. Conclusions have often poorly incorporated the economic values of the full range of environmental products and services supplied by these areas to the public, and to the landowners themselves. To compare the value of investment in oak savanna and traditional modes of production with alternative investments, it is important to understand all the components of that value to society. Here we review several investigations into oak woodland values, on and off-site, and to the public and the landowner.

Value of Commercial Production from Woodlands and Dehesa

The contributions of the three major commercial enterprises to the total net present value of California oak woodlands varies with the quality of the rangeland base *(fig. 3)* (Standiford and Howitt 1993), reflecting the focus on returns from beef. The contribution of various enterprises to the net operating margin in the Spanish dehesa for four case studies carried out in holm oak and holm and cork oak woodlands in the Monfrague Shire varies with site quality and the composition of the woodland (Campos-Palacín and others 2001), stemming from the complex relationship between tree composition, soils, and the diversity of income streams possible in the dehesa *(fig. 4)*.

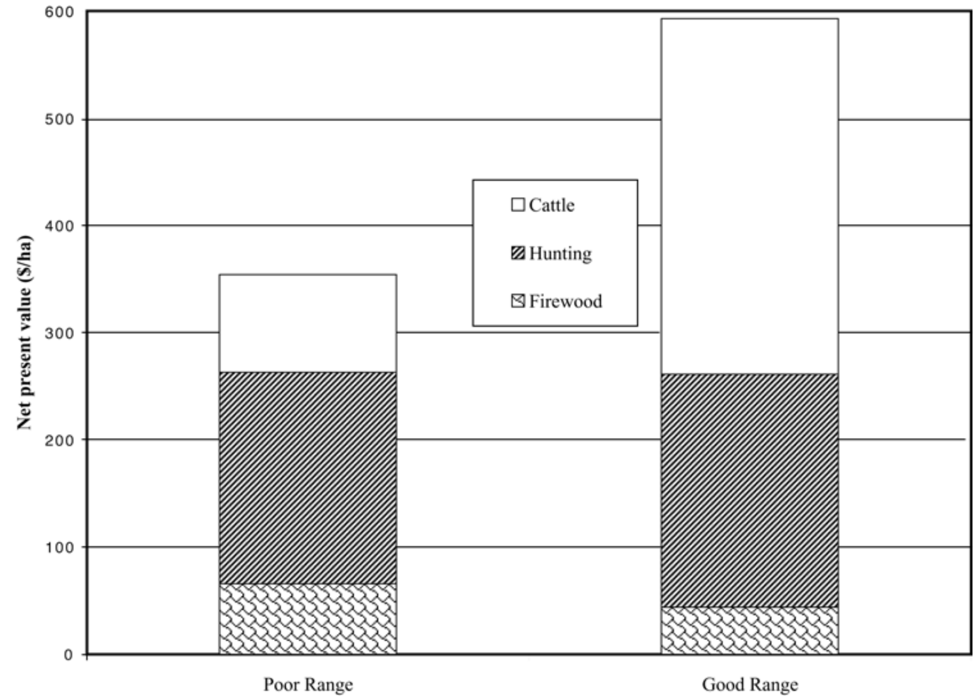

Figure 3—Net present value of Californian oak woodlands from various commercial enterprises, 1992 (Standiford and Howitt 1993).

In general, ranching with typical cow-calf enterprises has a positive economic value in California. In the Spanish dehesa, the margin for livestock from the case studies was negative, but grazing services (leased land) was positive. The negative economic value of livestock was compensated for by the European Union Common Agricultural Policy (CAP) subsidy for livestock production. In both countries, there is some indication that livestock producer goals and oak woodland management are becoming decoupled in some areas, as oak woodland and dehesa properties are purchased by new kinds of owners. There is increasing ownership by wealthier individuals with other sources of most of their household income. In California where speculative opportunities exist, purchase by developers and land speculators is common. However, tax breaks for keeping land in agricultural production mean these lands are often grazed.

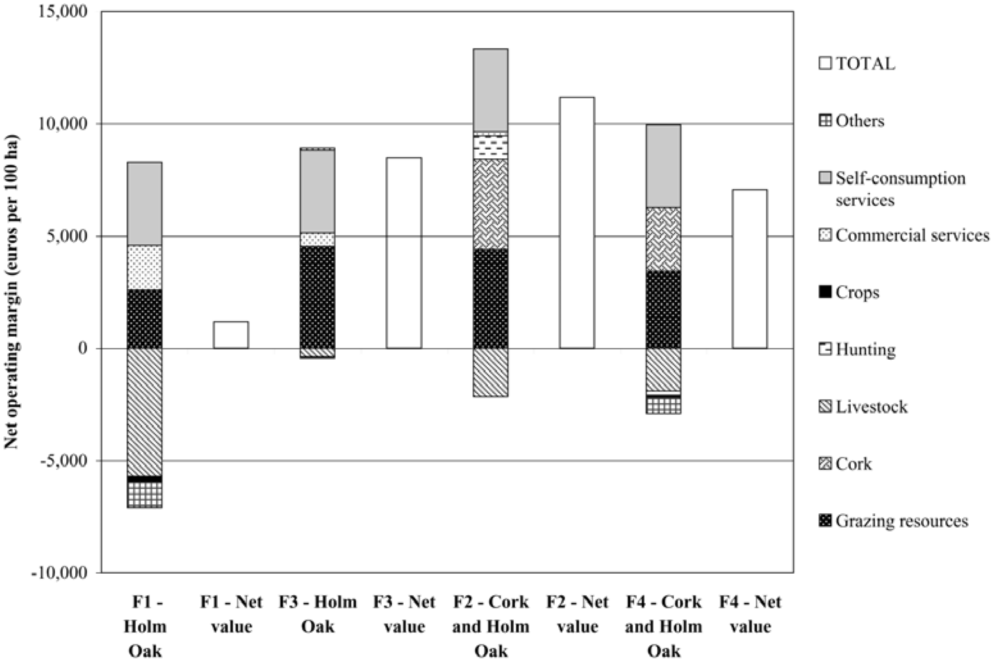

Figure 4—Net margin of various production values for four dehesa case studies in Monfrague Shire.

California studies of the value of hunting shows it has the potential to be an important enterprise for owners with fee hunting operations, ranging from 40 percent (on good range sites) to 70 percent (on poor range sites) of the total commercial value of the woodland. In Spain, for the four ranches interviewed, hunting was a significant economic enterprise for one. The economic contribution of wood harvesting is low when compared with cattle or hunting enterprises in California. A similar trend is observed in Spain on holm oak properties. However, when cork oaks are present, the value from the harvest of cork represents a significant contribution to value.

Conservation Values

One method for conserving oak woodlands is though land trust purchase of “development rights” from landowners, removing from the title the right of the landowner to develop or convert the property. Instead, the NGO-land trust holds this part of the title. The contribution of oak woodland open space from one such land trust area in southern California to community land and home value was evaluated using hedonic pricing. A decrease of 10 percent in the distance to the nearest oak stands and to the edge of the permanent open space land resulted in an increase of $4 million in total home value, and an increase of $16 million in total community land value (Standiford and Scott 2001), demonstrating the significant off-site benefits of open space areas and native oak woodland stands.

A study of public demand for environmental values in Monfrague National Park's oak dehesa ecosystems demonstrated their value to the Spanish public (Campos-Palacín 1996). The demand curve developed showed that the value of recreation and conservation services to dehesa visitors was high, and inversely related to an individual's frequency of visits.

Self-Consumption of Environmental Values

Important components of the full value of savanna ecosystems are the environmental and other benefits consumed by the landowner. Livestock producers in Spain and California place high value on their "way of life." California studies have shown that despite minimal profits or even losses when opportunity costs are considered, ranchers persist for the less tangible returns of ownership (Hargrave 1993 Huntsinger and others 1997, Sulak and Huntsinger 2002). And of course there are increasingly owners whose interests in owning the woodland are not at all related to the profitability of a livestock enterprise.

In Spain, recent studies have considered how a landowner's self-consumption of environmental services is incorporated into their private capital income. The concept of rancher self-consumption appeared in the scientific literature more than 25 years ago (Smith and Martin 1972, Torell and others 2001). Application of the concept to forest landowners has just recently emerged (Crabtree and Appleton 1992, Samuel and Thomas 1999). In Spain, self-consumption of environmental services has been quantified for the dehesa of Monfrague Shire (Mariscal and Campos-Palacín 2000). The results of detailed questionnaires of Monfrague landowners about management practices reveal that they are willing to lose a significant amount before selling their dehesa land, and that the smaller the property, the greater the proportion of the value they get from the property is self-consumed. They prefer to assure current and future self-consumption of recreational and environmental services from their dehesa.

This same phenomena was addressed in California bioeconomic studies by incorporating the concept of hedonic pricing (Standiford and Howitt 1992). A normative dynamic model of the full range of products supplied by oak woodlands (cattle, firewood, hunting), without including this concept of self-consumption, led to the conclusion that existing markets would lead to the clearing of oaks on rangelands. Although this was once quite common in the 1940s to 1970s (Bolsinger 1988), clearing has been rare in recent years. Oak woodland landowners commonly conduct partial harvesting with tree retention. The shortcomings of the normative model were a result of a failure to account for a landowner's utility from maintaining a certain stock of trees for their amenity and other non-market values. A positive mathematic programming (PMP) approach (Howitt 1995) was used to derive missing elements of the true costs of firewood harvest that were omitted from the normative model. This resulted in a firewood revenue model that combined market information with actual landowner behavior. The "cost" of overcutting firewood, or the self-consumption value of retaining trees, was derived. This specification gives a much better representation of expected landowner behavior.

Total Economic Value

It is clear that oak savanna landowners in Spain and California are not acting "rationally" according to normative economic assumptions and models. We would argue that their behavior is quite rational when all the components of value or "income" are accounted for. This has been addressed in studies of the dehesa by applying the concept of "total economic value." The essential feature of the total economic value model (Bateman 1992, Pearce 1993), proposed as an alternative to financial flow models, is that it extends income measurement to the monetary values associated with scarce environmental services *(table 2)*. The scarcity of these services translates to monetary value for oak woodland visitors and landowners.

Table 2—*Four dehesa case studies in Monfrague Shire: private total sustainable income (annual data from 1997/1998) (euros per 100 hectares).*

	Holm oak dehesa		Mixed holm and cork oaks	
Income source	**Case F1**	**Case F3**	**Case F2**	**Case F4**
Labour (LC)	9,754	8,855	2,669	4,639
Net operating margin (NOM)	1,173	8,481	11,173	7,046
Grazing resources	2,582	4,518	4,386	3,429
Cork			4,031	2,818
Livestock	-5,710	-392	-2,160	-1,912
Hunting			1,042	-188
Crops	-225	-47		-37
Commercial services	1,991	607	181	-47
Self-consumption services	3,696	3,696	3,696	3,696
Others	-1,162	99	-3	-713
Operating subsidies (OST)	24,114	3,367	-296	1,146
Net value added (NVAfc)	35,041	20,703	13,546	12,831
Capital gains (CG)	20,582	19,948	13,351	26,058
Capital income (CI)	45,869	31,796	24,228	34,250
Total sustainable income (TSI)	55,623	40,651	26,897	38,889

In addition to the ecological value of oak woodlands, including wildlife habitat, watershed, and carbon sequestration, and the commercially-marketed outputs from the woodlands, "option value" and "existence value" can also be defined. Option value is the visitor and landowner's willingness to pay to ensure continuous and lasting consumption of current environmental services. Existence value is not linked to active consumption, but to the consumer's perception that by protecting the resource he or she is ensuring conservation of threatened resources. These might include endangered species in Spain and California, and in Spain, autochthonous livestock species.

Results of detailed surveys of four dehesa estates in Monfrague Shire (Campos-Palacín and others 2001) include values for marketed commercial products, as well as self-consumption of environmental services, ecological function, option values such as legacy value, and existence values *(table 2* and *fig. 4)*. California production studies have not quantified the self-consumption of oak woodland environmental values. The positive policy modeling approach described above considers this effect with the hedonic pricing method, but has not quantified this as part of the total economic value of the property. Studies in Spain have shown the significant values of self-consumption. The omission of environmental service income in national assessments of dehesa values is a crucial undervaluation of dehesa contribution to private and social income levels. Capital gains, also omitted in national accountings, have been the dehesa's most important source of private income returns over the past 25 years. These same techniques of evaluating total economic value will be applied in California oak woodlands in future joint studies. This will help to more accurately portray the true value of oak woodland open space.

Institutional Capacity

In California, most oak woodlands are in private ownerships that evolved from Spanish or Mexican land grants, or the Homestead Act of 1862, or various other nineteenth century land disposal mechanisms. The woodlands are subject to many levels of oversight and regulation. Oak protection, land use, and development ordinances may affect a landowner's management at local and county levels. At the state level, water quality, fire protection, and timber harvest regulations may be a factor. Pro-active, incentive-based programs are rare. One of the few incentive programs is the California Land Conservation Act of 1965, or Williamson Act. This Act provides a property tax break to those who contract with the county not to develop their lands for ten years, and is automatically renewed each year until the landowner withdraws. The state provides funds to counties to reduce the loss in tax revenues. Approximately 70 percent of the oak woodlands of the state are under this type of contract (Huntsinger and others 1997), but it is acknowledged that it is not a long-term policy (McClaran and others 1985). A state sponsored voluntary education program appears to have contributed to a reduced rate of oak cutting over the last ten years, but in general, oak woodland landowners are hostile to government intervention (Huntsinger and others 1997).

Instead, non-governmental organizations are playing a growing role in conservation. The Nature Conservancy, local land trusts such as the Marin Agricultural Land Trust, and other privately-funded groups have brought significant oak woodland properties into land trusts and conservation easements. California has more land in conservation easements, surpassing 40 million ha, than any other state. Four percent of ranchers surveyed in two regions of California reported having some sort of conservation easement on their land (Liffmann and others 2001). There is an increasing recognition that maintaining extensive ranching operations may be cost-effective large-scale landscape conservation. Governmental action affecting oaks directly has mostly been at the municipal level, with ordinances protecting specific kinds or sizes of trees within town limits. Saving and Greenwood (2002) offer insight into the very limited efficacy of these approaches.

In Spain, the extensive transhumance, political and demographic upheavals, and property changes that occurred in the Middle Ages favored creation of large extensive farms under the military, clergy, and nobility (Trujillo and Mata 2001). A complex of land title reforms in the nineteenth century shifted these and many common properties into private hands. A proactive program of dehesa conservation has been developed at the provincial, national, and pan-European levels, commonly providing direct subsidies to agricultural producers. Typically, dehesa landowners get a quarter to a third of their income as a subsidy. In recent years, there has been a shift away from European Union (E.U.), "Common Agricultural Policy" (CAP) subsidies that emphasize intensification of livestock production. There is a deepening interest in the maintenance and viability of what is described as "low intensity agriculture," of which the dehesa landscapes of Spain and Portugal and many of the grazed landscapes of France, Hungary, and other E.U. states are examples. These "less productive" forms of agriculture are to be supported in an effort to reduce environmental degradation, and to provide employment for remnant local community members in picturesque (and perhaps ecotourism-friendly) modes of production. In the long term, they may result in greater levels of rural self-sufficiency.

In Spain it is widely acknowledged that the dehesa is of cultural as well as environmental import. With so little public land, the need to conserve privately owned landscapes is well-recognized. National Preserves normally encompass active agricultural enterprises. In addition, there is a long tradition of overlapping property rights. Villages often had or have usufructuary rights of various kinds to estate lands; livestock migration trails and some village lands were and are used and/or owned in common, and so forth. There is not the same inclination to assert such individualistic private landownership in Spain. It is not a reach to recognize a public interest, and a responsibility to the public, in private landownership. Some conservation initiatives draw on the Spanish regional pride that is re-asserting itself after Franco era suppression. Beef, ham, and cheeses carry regional government regulated appellations similar to those of U.S. wines. Premium prices can be charged for some products, such as acorn-fed hams, helping dehesa profits.

In California, significant oak woodlands have the potential for conversion to vineyards and other crops (Heaton and Merenlender 2000). Land use planning policies are not coordinated at local, county, regional or state levels, and many hardwood rangeland areas permit subdivision of large parcels into ranchettes of 5 to 40 acres, or large urban developments (Doak 1989). This creates an increasing economic tension for the remaining ranch owners to shift out of ranching. For example, in the central coast, grazing land value may be less than 10 percent of the value of the land for alternative uses with higher environmental costs (Standiford 1999). Previous work has shown that while retained oak trees in rural subdivisions have been shown to contribute up to 27 percent of the value of the property (Diamond and others 1987), they seldom survive the transition in land use. Since this tree value is typically not realized until the land is sold for development and subdivided, many oaks are lost even though they would have significant long-term value.

In Spain, livestock rearing subsidies still constitute the main source of public funds going to dehesa owners. Animal numbers are at an all-time high, threatening oak regeneration. Yet today there are aggressive and comprehensive strategies to minimize land use conversion in the dehesa. The European Commission, the Spanish government, and even regional authorities, can intervene in dehesa land use. In 1985, the European Economic Community (EEC) integrated nature conservation measures in CAP reform for the first time. The new CAP is aimed towards land uses compatible with nature and cultural heritage conservation. Trading rules for certain strategic rural goods can be specified under the new CAP. Subsidies for production technologies compatible with the protection of the bio-physical environment, natural area conservation, and reforestation of agricultural land with oaks are also clear examples of the new kinds of EU interventions. EU subsidies cover plantation costs, maintenance costs through the first 5 years, and provide a premium to cover the loss of income resulting from reforestation. By December of 1998, more than half a million hectares were artificially reforested in Spain. A stunning 53,563 ha were reforested with holm oak, 21,353 ha with cork oak, 42,391 ha with mixed plantations of cork oak and holm oak, and another 108,681 ha with these two species mixed with other tree species. Additionally, 82,405 ha of mature cork oaks have also been improved under these programs.[6]

Future Work

Oak savanna conservation has three facets: extent, regeneration, and stewardship. The needs in each area vary in priority and importance at local, regional, and national scales. In Spain, the focus of effort is shifting to the gradual attrition of the trees at least partly due to changes in management starting in the 1960s, as government intervention has stabilized woodland extent. The E.U.'s forthcoming regulatory Natura 2000 network will soon replace or complement regional and national authority in environmental policymaking. It remains unknown how successful regeneration was under traditional management, so restoration of traditional practice may not be sufficient. In California, a lack of coordination in planning at local, regional, and state scales has resulted in haphazard and increasing conversion of oak woodlands for housing and vineyards. Changes in the oak woodlands since the mid-nineteenth century are believed to be contributing to a lack of oak regeneration in many areas.

Oak woodlands in both California and Spain have been undervalued by traditional agricultural production models. New approaches to evaluating the self-consumption of environmental services, and the quantification of the real utility of amenity values offer promising approaches to better represent their value to landowners. A positive mathematical programming approach using optimal control policy runs is being initiated in Spain. Detailed questionnaires and case studies of will be carried out in California to quantify self-consumption of environmental resources.

California studies of oak woodland open space shows their effect on overall community values. This provides information on the supply side of open space. Studies in Spain on public demand curves for recreation and conservation values shows the demand side for oak open space values. Future work will apply demand and supply studies in both countries.

Given differences in ecological dynamics and public policy, how can the full range of oak woodland values be analyzed and represented in ways that will stimulate their conservation? The concept of "total economic value" in Spain has contributed to a fuller appreciation of low value agriculture in the public policy arena. In California, it is less certain where a full accounting of value will find channels for application. Collaboration between Spain and California offers an opportunity to contrast the effectiveness of public subsidy approaches widely used in Europe to private investments through land trusts and other means. Trends in investment in conservation and their effect on land use patterns, economic functioning, and the ecological structure and function of oak savanna will be compared.

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[6] Unpublished data on file, Spanish Ministry of Agriculture, Fish, and Food.

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A Comparison of the History and Management of Oak Woodlands in Britain and California[1]

Douglas McCreary[2] and Gary Kerr[3]

Abstract

Hardwood forests are principal features of the landscape of both California and Britain and indigenous oak species are important components. In both locales these “oak woodlands” have historically provided a wide variety of commercial and non-commercial products and benefits and are deeply valued and appreciated by those who live in and around them. However, human-induced impacts have reduced the original forest cover in each area and there is concern that oak woodlands are still at risk, especially from impacts associated with increasing residential land-use conversion. While there are similarities in how these woodlands have been managed and used in both locations, there are also striking differences. In Britain the impacts to woodlands have occurred over millennia, rather than centuries, and the reduction in original forest cover has been much more extensive. As a result, the current management strategy includes an aggressive effort to increase woodland cover through government funded planting programs. In California, on the other hand, significant losses of oak woodlands have only occurred in the last two centuries and on a percentage basis, have been far less. Current management focuses on conserving existing oak woodlands through programs of research and education. Hopefully, in both California and Britain these efforts will be successful and help ensure that oak woodlands are sustained and even expanded, so that future generations will have the opportunity to use and appreciate them.

Introduction

Both Britain and California have large areas of hardwood forest dominated by native oaks. In California, these areas are often referred to as “oak woodlands.” However, this term is not commonly used to classify woodlands in Britain. For historical reasons, the main distinction in Britain is between “conifers,” “broadleaved,” and “mixed” woodlands. However, within the broadleaved woodland, oak is the most important species and was the principal species in 31 percent of the area of broadleaved forest at the last census in 1979 *(table 1)*.

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[1] An abbreviated version of this paper was presented at the Fifth Symposium on Oak Woodlands: Oaks in California’s Changing Landscape, October 22-25, 2001, San Diego, California.

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Table 1—*Species composition of broadleaved forests in Britain in 1979.*[1]

Principal species	Area (1,000 acres)	pct
Quercus robur and *Q. petraea*	425	31
Fagus sylvatica	183	13
Acer pseudoplatanus	122	9
Fraxinus excelsior	172	12
Betula spp.	168	12
Populus spp.	34	2
Castanea sativa	24	2
Ulmus spp.	23	2
Others	72	5
Mixed	161	12
Total broadleaves[1]	1,384	100

[1] Between 1979 and 1998 the total area of broadleaves has increased by 271,000 acres. Source: Locke (1982)

The two species of native oaks in Britain are English oak (*Quercus robur* L.) and sessile oak (*Q. petraea* Matt. Liebl.) (Morris and Perring 1974), both deciduous and members of the white oak sub-genera. English oak is generally associated with the warmer and drier south and east of Britain, and sessile oak, the wetter and cooler north and west of Britain. However, the long history of management, the fact that the species readily hybridise, and the large amount of seed imported from the rest of Europe have led to considerable mixing of the two species. In fact there is some discussion whether they are distinct species (Ferris and others 1998).

By comparison, California has 21 species of native oaks, ranging in size from massive valley oaks (*Quercus lobata*) with wide-spreading canopies, to shrublike huckleberry oaks (*Quercus vaccinifolia* Kellogg) that grow less than a few feet tall (Pavlik and others 1995). About half of the California species are deciduous and half are evergreen. The breakdown of hardwood forests in California by principal species and acreage is listed in *table 2*. Stand characteristics in woodlands can vary considerably depending upon climate, site conditions, species composition, and management history. Compared to more diverse higher elevation conifer forests, however, many of these woodlands are very open and only consist of two or three tree species. Tree growth is often slow, especially on drier sites with shallow soils, and there is concern that in many woodland stands, natural regeneration of several oak species may not be adequate to replace mortality.

Table 2—*Species composition of hardwood forests in California in 1985.*[1]

Principal species	Area (1,000 acres)	pct
Quercus douglasii	1,691	23
Quercus agrifolia	1,176	16
Quercus crysolepis	1,102	15
Quercus wislizenni	735	10
Quercus garryanna	588	8
Arbutus menzisii	588	8
Quercus kelloggii	441	6
Quercus lobata.	221	3
Quercus engelmannii	39	Trace
Other non-oaks	808	11
Total hardwoods	7,351	100

[1] From Bolsinger (1988)

The climate of Britain is generally oceanic, warmer than similar continental areas at the same latitude because of the effects of the Gulf Stream. However, there are large regional differences in climate between the southeast and northwest of the country, with southern England much warmer and drier than mountainous northern areas. In contrast to Britain, the main climatic differences in the oak woodlands of California ane from east to west. Coastal areas are greatly influenced by the ocean and are cooler and moister than areas further inland. However, the climate for both coastal and inland oak woodlands is considered Mediterranean with the vast majority of rain falling in the fall and winter, and a lengthy dry period, often extending from May until September.

History of Woodland Management in Britain

It is estimated that 5,000 years ago forests in Britain covered as much as 95 percent of the land area. Most of these forests were comprised of mixtures of hardwoods, including the two native oak species. The Neolithic people that populated Britain between 5,000 BC and the arrival of the Romans certainly reduced forest cover, though it is difficult to accurately say how much. They probably used fire to herd game to areas where they could be killed, as well as to improve grazing for both wild and domestic animals. They also cleared large areas for agriculture. Therefore, when the Romans arrived in the first century AD, it is believed that forest cover had already been reduced by about a third from original levels. Increased population in the Roman Era, however, and the need for more food, building materials, and fuel contributed to further forest loss. These losses were exacerbated by intensive grazing that often inhibited the success of young tree seedlings.

After the Norman invasion in the 11th century, the first large scale inventory of forests in Britain was recorded in the Domesday Book, which indicated that forest cover at that time had decreased to just 15 percent of the land area. After that, losses continued at a rapid rate, as demand for wood mounted and grazing intensified. Large quantities of wood were required for ship building, construction of buildings, fuel, and for other industrial uses, including evaporation of brine for salt, glass works, and the smelting of iron. The demand for large and small size timber gave rise to the practice of coppicing, which is the repeated cutting of the above-ground part of a tree on a 5- to 15-year cycle, depending on the size of timber required. Areas were managed as pure coppice or in combination with large trees as "coppice with standards." In many areas oak was the most common species of large "standard" trees, but was also worked as coppice. The harvested wood was utilized for a variety of products including tools, implement handles, fencing and fuel. An important consideration for successful coppice management was to limit access by grazing animals, at least during the interval when the new coppice shoots were small and becoming established. Unfortunately, grazing was often not adequately controlled, resulting in poor coppice growth and inadequate natural regeneration to replenish stands, causing further woodland loss. By the beginning of the 20th century, forest cover had decreased to just 5 percent of the total land area.

During the 19th and early 20th centuries Britain relied heavily on imported timber, particularly from its Empire. However, the First World War made it clear how dependent the country was on imported timber and its vulnerability to naval blockades. Because imports were restricted, many existing woodlands were heavily exploited. This led to the formation of the Forestry Commission in 1919 which set the objective of establishing a strategic reserve of timber in the event of another major conflict. Unfortunately, the Second World War occurred before much of the new planting had started to produce timber, so again the existing woodlands were exploited and many were felled.

The management focus of the newly created woodlands, and forestry policy for much of the twentieth century, was plantation silviculture using mainly non-native conifer species. This set the agenda for British forestry for many years. However, in the 1980s, there was a major review of policy on broadleaved woodlands. This led to a string of measures to protect existing broadleaved woodland, particularly ancient semi-natural woodland, and incentives to create new broadleaved woodlands (Forestry Commission 1985).

Today the total forest cover in Britain is estimated to be a little over 10 percent, with approximately two thirds of this consisting of conifers. Conifer planting, however, has been greatly reduced in the last decade since it is now recognized that while these plantations efficiently grow wood products, they do not provide the same range of values inherent in native woodlands, including wildlife habitat, aesthetics, recreational opportunities, and vital ecological functions. Recognizing the importance of hardwood forests and their relative scarcity, the government initiated an aggressive policy to sustain existing woodlands and expand tree cover. By 1996 there were four acres of broadleaves planted for every one acre of conifers. The Forestry Commission owns 48 percent of all coniferous woodlands, but only 7 percent of broadleaved woodlands, so the Commission works with private landowners. As described below, the conservation and planting efforts in Britain are encouraged through a range of grant programs funded from both the public and private sector.

History of Woodland Management in California

In California, intensive use and management of forest resources began later than in Britain. While native peoples occupied the area now known as California for 10,000 years, they probably did not reduce forest cover to a great extent. The common perception is that Native Americans or Indians lived in harmony with nature, doing little to manipulate it. However, there is increasing evidence that they did actively manage woodlands—especially by the use of fire (Blackburn and Anderson 1993). The understory was regularly burned for a variety of reasons, including facilitating access, stimulating new plant growth, improving habitat for game, making it easier to collect acorns, and killing insects that damaged acorn crops. Areas were also cultivated to promote edible bulb production and the yield of materials from plants used in basket making was maintained by burning and pruning. But Native Americans did not convert forests to agriculture as Neolithic people did in Britain. However, burning woodlands probably resulted in the creation and maintenance of cohorts of large oak trees, since many smaller trees would have been killed by fires, and there likely would have been efforts to protect large trees since they are generally the best acorn producers. In the lower elevation valleys, repeated burning would also have promoted more open savannah-like stands with widely spaced valley oaks. This is certainly what the earliest explorers reported seeing in California in the early 19th century.

Starting in the Mission Period in the 18th century, grazing was introduced to the state. Livestock no doubt hampered natural regeneration of oaks through repeated browsing of young seedlings, but the demand for wood during this period remained relatively small, and impacts to existing stands of trees were not serious or extensive. However, both sheep and cattle helped spread the seeds of introduced Mediterranean annuals, which were brought to California for animal feed and forage, and these plants increasingly came to dominate the understory of oak woodlands. This conversion of range vegetation from predominantly native perennial bunch grasses to introduced annuals has been suggested as a possible cause of reduced oak regeneration in certain locales today (Welker and Menke 1987).

The greatest impacts to oak woodlands resulted from the large increase in population and widespread settlement of California during and after the Gold Rush in the mid-1800s. Large areas were cleared for agriculture, especially on the deep alluvial soils of the Central Valley of the state that had previously supported complex riparian communities, often dominated by massive valley oaks. Vast numbers of cattle were also brought into the state, including the English breeds, Hereford and Angus, that dominate range livestock herds today. Many trees were also felled to fuel railroads, steamships, and mines, as well as to supply domestic heating needs, and there was an increased incidence of wildfires. These impacts were often localized near settlements or adjacent to railroads or navigable rivers, and remoter areas were largely unaffected. Interestingly, unlike Britain, the use of oaks and other hardwoods for building materials was somewhat limited since abundant native conifers were generally preferred as a source of lumber. While all of these impacts seriously changed the landscape of the state, California was still a large area with relatively few people, so on a statewide percentage basis, the woodland forest cover lost during the 19th century was relatively small compared to what had occurred in Britain.

In the 20th century impacts to the woodland resources in California continued. Large water diversions on major rivers significantly altered hydrologic regimes, and the ensuing environmental changes adversely affected species such as valley oak that were adapted to wet conditions and periodic flooding. Fire suppression activities also greatly reduced fire frequencies in many areas and caused a build-up of combustible fuels, increasing the threat of large-scale catastrophic fires. Removing trees on woodlands for "range improvement" was widespread—especially after the Second World War—and approximately a million acres of oak woodland were converted to treeless pastureland between 1945 and 1973 (Bolsinger 1988). Losses from residential and commercial development also increased as cities expanded and previously rural areas were developed. In the 1970s and 80s there were also increases in firewood harvesting—especially in the Northern Sacramento Valley—as more and more people turned to wood to heat their homes after fuel prices went up dramatically following the Arab oil embargo. By the mid-1980s an inventory of hardwood forest types throughout California comparing total acreage in 1945 to 1985 found that the total area had decreased during this interval by 4 percent to a little over 10 million acres (Bolsinger 1988), with 77 percent of this land in private ownership.

Today in California, many of the threats and impacts described above have been reduced. There is almost no clearing of trees to improve rangeland now, and firewood harvesting has stabilized or decreased. Even where large areas are harvested for firewood, there is a much greater tendency now to thin stands and leave a substantial canopy to provide shade for livestock, cover for wildlife, and a much more desirable visual landscape. However, the population of the state continues to grow and residential and commercial development is still taking a heavy toll on woodlands in some areas. Cities are continually expanding outwards and people are moving into previously rural areas, largely because they value so highly the amenity values that the woodlands in these areas provide. Also, as the wine industry has experienced a boom with increased prices for wine grapes, conversions of oak woodlands to vineyards have gone up in the last decade in portions of the state. Concern about this change in land use has not gone unnoticed and several highly visible conversions of woodlands to vineyards have galvanized public support for increased state and local regulation of oak harvesting. There is also concern today about poor natural regeneration of several oak species and whether oak woodlands can be managed sustainably.

Values of Woodlands in Britain Today

Throughout the last 5,000 years, woodlands in Britain have provided essential wood products used for energy, tools and building materials. These areas have also provided habitat for game, as well as locations where grazing by domestic livestock could take place. While the production of wood products from woodlands is still important today, other values of woodlands are now equally, if not more, important. Forests have always been sanctuaries where people could retreat for escape and solitude. As wooded areas have become scarcer in relation to numbers of people in the country, and the relative rarity of large blocks of undeveloped natural land has increased, the value of existing woodlands to provide recreational opportunities has increased. Such areas are especially critical near cities where opportunities to experience natural landscapes are so limited. In general, there is much greater access to forested areas in Britain than in California, since public walking paths in wooded areas have been used for centuries and recent laws promoted by "rambling" (hiking) organizations have resulted in greater access for the general public within many private landholdings.

Woodlands also provide critical wildlife habitat. Many animals are dependent on the food and shelter provided in woodlands, and significant increases or decreases in amount of this habitat type can drastically influence species presence and abundance. In contrast to agricultural fields, which are very limited in structural diversity, woodlands provide a much wider array of habitat elements that can support larger numbers of species. Increases in the numbers and types of wildlife also increase the opportunities for people to see these animals, which is a highly valued recreational experience.

Even when people are not actually utilizing woodlands for hiking, hunting, or wildlife viewing, the presence of these areas can improve the quality of life for nearby residents by providing a desirable visual landscape. Trees enhance the beauty of the countryside and can screen housing developments or industrial complexes. Trees can also reduce noise levels and help filter out pollution.

Finally, while the value of the actual wood products that are extracted from woodlands is often relatively small compared to the other values these areas provide, ensuring a continual supply of wood products through planting programs also provides employment and helps sustain rural economies.

Values of Woodlands in California

The cultural values of oak woodlands in California are similar to those in Britain, and the areas where oaks grow are tremendously valued from an aesthetic standpoint. To many residents and non-residents alike, golden brown hills dotted with gnarled oak trees epitomize what California looks like, and native oaks symbolize important values—strength, beauty, adaptability and longevity. Today woodlands provide sites where people can go and escape the crowded cities if they have public access. Such experiences are rated highly since they provide opportunities to get away, experience nature, and find peace and solitude. Recreational activities vary greatly but include hiking, picnicking, camping, wildlife viewing, mountain biking, hunting and fishing. In addition, many Californians appreciate woodlands simply by driving through them on public roads.

As in Britain, oak woodlands are known to provide critical habitat to a rich and diverse assortment of wildlife. More than half of the 600-plus species of terrestrial vertebrates in California utilize oak woodlands at some time during the year, and the food and shelter provided are essential to their survival. This is a higher number of species than in any of the other habitat type in the state.

Finally, the management of oak woodlands is critical in protecting watersheds and ensuring the quality of water resources. The majority of the state's water is stored as snow pack in high elevation mountains and then flows through oak woodlands on its way to the streams and rivers which support fisheries, farms, and cities. Preventing erosion and sedimentation, providing micro-climate buffering, and furnishing necessary nutrients for in-stream fauna are all critical attributes of robust oak woodlands.

Woodland Conservation in Britain Today

As stated above, woodland loss has been extensive in England. Yet the values hardwood forests provide are increasingly recognized and appreciated. Consequently there has been widespread support for efforts to "bring back" broadleaved forests through government supported planting programs, and property owners can receive generous grants by undertaking these efforts. The two main aims of the Government's current forestry policy are (a) sustainable management of existing woodlands, and (b) expansion of tree cover to increase the many diverse benefits that woodlands provide (Anonymous 1991). The Forestry Commission implements this policy with a mixture of legal powers (from the Forestry Act 1967) and financial incentives. The most important legal power is that tree felling is regulated and a licence is required if an owner wishes to fell more than 175 cubic feet of wood in any calendar quarter. Nearly all licenses granted are conditional on the area being replanted, making it very difficult to convert forests to other land uses.

Generous financial incentives are also available to encourage policy objectives increasingly being targeted at public benefits. For example, in certain areas it is possible to get a grant of £1175 ($1,700) per acre for tree planting, plus additional annual payments. For example, planting grants for broadleaved forests are $800 per acre. As a rule, 940 trees per acre must be planted and the trees cannot be harvested for at least 30 years. In addition, there can be a supplement of $350 per acre if the planting site is on good quality land. Finally, an additional $550 per acre is paid to the landowner if they are willing to provide access to the public. In addition, annual payments of up to $175 per year for 15 years are available if land is taken out of agriculture. Money can also be paid to:

- Safeguard or enhance the existing special environment value of a woodland;
- Improve woodlands which are below current environmental standards;
- Work to help encourage informal public recreation in existing woodland;
- Encourage natural regeneration through fencing, etc.

In addition to increasing amenity values, these programs are also designed to bring woodlands which are undermanaged or of low commercial value back into production, creating jobs and revitalizing rural areas where industries have moved out or agriculture has become depressed. The sale of wood products from these newly created forests can be an important benefit to rural areas that have come on hard economic times.

Property owners can also receive funding from a wide range of complementary sources including central and local governments, the European lottery, Millennium funds, and the landfill tax. Private philanthropists have also joined in supporting tree planting, including millionaire Felix Dennis, who was recently reported to be spending $290 million of his own money to plant broadleaves on 30,000 acres (Ahuja 2001). Because of the generous financial incentives to plant hardwoods and restore woodlands, restoration of broadleaved woodlands has been very successful. Between 1994 and 1998 the Forestry Commission Woodland Grant Scheme approved broadleaved planting of approximately 70,000 acres per year. The long-term goal of these programs is to double the forest cover (to 20 percent) in the next half century.

Woodland Conservation in California

Prior to 1980, oak trees in California were often considered weeds by commodity-oriented landowners and public agencies charged with improving production, and there was little concern about conserving woodland habitats. However, in the 1980s, widespread firewood harvesting and an increased public and professional concern about large-scale wildlife habitats led the California State Board of Forestry to re-examine its policies for oak woodlands. There was fear that harvesting in sensitive watersheds might cause erosion problems, and that biomass-fueled power plants might rely on material from hardwood rangelands, resulting in extensive areas of clearing. There was also concern that removal of black oak in high elevation conifer forests would adversely affect migrating deer herds (Pillsbury 1983).

The Board of Forestry appointed two task forces to examine the issues related to the management of oak woodlands and to make recommendations about how to resolve them. There was not unanimous agreement about how to proceed. On the one hand there were those who called for state regulation on hardwood rangelands so that any harvesting would fall under the jurisdiction of the State Forest Practices Act. To accomplish this, hardwoods would have to be declared commercial species. Proponents felt that only by imposing rules regulating tree removal could potential abuses be avoided. On the other side were many private owners of oak woodlands, including livestock ranchers, who were not eager to have another level of bureaucracy and red-tape imposed on them. They pointed out that state regulation certainly hadn't eliminated all management problems in conifer forests, and that most ranchers had a strong land ethic and were good stewards of their property. They wanted a voluntary approach. In 1986, the Board of Forestry decided that it needed more information about the biology and management of oak woodlands and agreed to support the formation of the Integrated Hardwood Range Management Program (IHRMP) to address oak conservation issues in the state (Passof 1987). This Program was a cooperative effort between the University of California, the California Department of Forestry and Fire Protection, and the California Department of Fish and Game, to encourage long-term conservation through both research and education efforts. The research would focus on understanding the critical biological and management factors potentially threatening the long-term sustainability of oak woodlands. The educational aspect was designed to quickly disseminate any research findings to owners and managers of woodland properties so that they would have the most current, scientifically-based information at their disposal to guide management. The state also encouraged the counties to take actions necessary to ensure that oak woodland resources were not threatened and were managed sustainably. The Board felt that a non-centralized approach would be more effective since many of the threats to oaks were local in nature and local jurisdictions were better positioned to address specific needs. Local approaches have included ordinances, stipulations in general plans, and voluntary guidelines endorsed by county boards of supervisors.

In addition to these efforts, non-profit conservation organizations including the California Oak Foundation and the California Native Plant Society have are also become actively involved in promoting woodland conservation through outreach and education, as well as political lobbying.

Conclusions

The approaches for managing oak woodlands in Britain and California today are very different. In Britain, there are strict rules about harvesting existing hardwood stands and well-funded programs to promote the planting of oaks and other broadleaved species. There are also programs to offset costs for converting existing conifer forests to more natural woodlands. These planting programs aim to re-establish native forests in areas where they historically flourished but have been converted to other uses. Though costly, these programs are widely supported by the public who view woodlands as part of their natural heritage and rate highly the amenity values they provide. These programs are also ambitious in that they are designed to double the acreage of forests in Britain over the next half century.

In California, by contrast, oak woodland management today is primarily concerned with minimizing losses to existing woodlands and there are no statewide regulations regarding harvesting or tree removal. There are also few financial incentives to expand hardwood forests through planting, although planting is often required as mitigation for development and some conservation organizations such as The Nature Conservancy have large oak planting projects. Local governments are responsible for implementing rules or programs addressing oak woodland conservation, and these approaches vary widely, depending on local threats to the resource (i.e. firewood harvesting, agricultural conversions, development pressures) and the local political climate. There is an extensive program of research and education, with mechanisms for addressing emerging threats and issues and formulating management recommendations to promote oak woodland conservation. There are also non-profit organizations that advocate tree protection and lobby against activities that they view as threatening the resource.

The differences in the oak woodland management approaches currently in place in Britain and California are strongly influenced by history. In Britain oak woodland losses have been so great that only small remnant stands remain and there is a concerted effort to return the landscape to what it looked like in an earlier era. In California, on the other hand, we still have vast acreages of intact, but altered, woodlands, and there is less of a sense of urgency in protecting what is left.

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Riparian Valley Oak (*Quercus lobata*) Forest Restoration on the Middle Sacramento River, California[1]

F. Thomas Griggs[2] and Gregory H. Golet[3]

Abstract

In 1989 The Nature Conservancy initiated a riparian horticultural restoration program on the floodplain of the middle Sacramento River, California. At nearly all restoration sites Valley oak (*Quercus lobata* Nee) comprised a major component of the planting design. Valley oaks are a keystone tree species of lowland floodplain habitats in California's Central Valley, contributing greatly to the structural and biological diversity of riparian forests in the region. Here we present preliminary comparisons of survival and structural development of oaks planted as acorns at six sites from 1990 to 1994. Our focus is on how the plants responded to natural site conditions following the cessation of maintenance activities (including irrigation and weed control). Initial comparisons demonstrate considerable variability among sites in survival and structural development (i.e., stem diameter, canopy cover, and dominance). Although we were able to ascribe some of this variability to known physical and biological differences in site conditions (e.g., soil type, herbivore pressure), furthering our understanding of factors that affect valley oaks on the Sacramento River floodplain will require additional study and more detailed assessments of site conditions.

Introduction

Prior to European contact riparian forests of the Sacramento Valley covered over 800,000 acres (Katibah 1984). Valley oaks were a primary component of these forests, typically growing on fine-textured soils on the higher portions of the floodplain. They are deciduous, quick growing trees that thrive in hot, sunny conditions when supplied with sufficient water and nutrients. The largest individuals have trunks of over 2 m in diameter, and typically support sets of massive craggy limbs soaring upwards of 30 m. Valley oak riparian forest has the most complex structure of any vegetation type in California, and as a result, is among the most diverse in terms of the animal life it supports (Pavlik and others 2000).

In the late 1800s the rich soils of the Sacramento River floodplain were cleared of riparian vegetation to provide fencing, lumber, fuel for steamships, and open areas for agriculture (Scott and Marquiss 1984, Thompson 1961). In 1945 Shasta Dam was completed, bringing with it a reduction in the threat of catastrophic flooding and an associated increase in conversion of lower floodplain forests to farmlands. Today less

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[1] An abbreviated version of this paper was presented at the Fifth Symposium on Oak Woodlands: Oaks in California's Changing Landscape, October 22-25, 2001, San Diego, California.

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than 20,000 acres of riparian woodlands remain, mostly in degraded condition (Hunter and others 1999, Katibah 1984).

In 1989, The Nature Conservancy (TNC) initiated the Sacramento River Project with the goal of restoring properties adjacent to the channel of the Sacramento River to wildlife habitat for the benefit of native species (Reiner and Griggs 1989). This project, which is entirely driven by willing sellers, provides an opportunity for growers to escape the economic burden of farming low on the river's floodplain. As was made evident by four major recent floods, including the January 1997 event (one of the most costly and geographically extensive flood disasters in the state's history), the present flood-control system of the middle Sacramento River watershed still cannot guarantee protection to those who invest in agriculture close to the river (US Army Corps of Engineers 1999). The erosion and deposition of sediment associated with high flow events translate into onerous maintenance costs for growers whose fields become inundated (Ginny 2001). Today, numerous state and federal agencies are implementing riparian restoration projects on flood-prone lands along the river. These include the U.S. Fish and Wildlife Service, the U.S. Army Corps of Engineers, the U.S. Bureau of Reclamation, the USDI Bureau of Land Management, the California Department of Fish and Game, the California Department of Water Resources, and the California Department of Parks and Recreation. As well, several local watershed conservancies and land trusts are actively engaged in restoration efforts in the area.

Although it is widely recognized that revitalizing degraded river systems requires the restoration of natural river processes (Poff and others 1997), horticultural restoration can provide complementary benefits, particularly in instances where there is a critical need for increased habitat in the near term. This is certainly the case in the Central Valley, where over 90 percent of the riparian forests have been lost in the last two centuries (see Golet and others, in press, for a map comparing current and historical riparian habitat in the Sacramento River Project Area). Horticultural restoration on a wide scale is a new practice, however, and as such is in need of evaluation. As a first step in this process Alpert and others (1999) reported initial results of horticultural restoration efforts at several of TNCs riparian restoration projects following three years of maintenance. Here we provide a brief follow up to Alpert and others' study by characterizing the development of valley oaks following the cessation of maintenance activities. The trees we studied were 7 to 11 years old, and had been growing unattended for 4 to 7 years.

Methods

Table 1 presents the size, year planted, and year of last maintenance of each of the six restoration sites sampled in this study. All sites are located on the mainstem of the Sacramento River between Corning and Princeton *(fig. 1).*

Each restoration site was planted with different proportions of ten woody species (see Alpert and others 1999) based upon limited available information on initial soil texture and stratification, depth to ground water, and frequency of flooding. For example, sites with soils composed of a high proportions of sands with higher relative water tables were planted with more willows (*Salix* spp.) and cottonwoods (*Populus fremontii*) and less oaks and elderberries (*Sambucus* *mexicana*) than sites with fine textured silty-loam soils and greater depths to ground water. In addition, each site supported different weed communities and had different densities of herbivores (e.g., rodents and deer). Differences in the initial responses of planted species to site conditions led to differences in maintenance activities (e.g., irrigation and weed control). Obviously, these sites cannot be considered as true replicates of one another in an experimental sense. Nonetheless, comparing them is useful, as evaluating past efforts can inform us how to better do restoration the future.

Table 1—*Description of riparian restoration units on the Sacramento River. RM stands for river mile, and L and R refer to left bank and right bank (looking downstream) respectively.*

Site	Location	Size	Year planted	Last maintenance
Princeton	RM 164L	16 ha	1993	1995
Sam	RM 190R	28 ha	1992	1994
Vista 1	RM 215.5L	9.6 ha	1993	1995
Vista 2	RM 216L	53.6 ha	1994	1996
Kopta 2	RM 220R	28 ha	1990	1992
Kopta 3	RM 220.5R	17.2 ha	1992	1993

We collected data at the restoration sites during July and August 2001. For each site we calculated density, percent survival, canopy cover (m^2 per ha), mean diameter at breast height (dbh, in mm) and dominance (cm^2 stem area at breast height per ha). Sampling was based upon the point-centered quarter method as described in Mueller-Dubois and Ellenberg (1974). We used a simple random sampling protocol (Scheaffer 1990) to select starting points for transects along borders of the restoration sites. Starting points were selected in such a way that every point had an equal probability of being chosen. We used a hand-held compass to stay on transect and sampled points at regular intervals. Intervals between sampling points varied from 30 to 100 m in accordance with the size of the sites (shorter spacings between sampling points were opted for at smaller sites to bolster sample size). A minimum of 10 points were sampled at each site. Upon reaching the sampling points, we placed the compass on a level surface and used its readings to divide the horizontal plane into four quadrants. Within each quadrant, the nearest woody tree or shrub of all species was identified, and the distance of this individual to the sampling point center was measured. For each of these plants of breast height or taller, we measured the dbh of the largest stem. Thus, four species identifications, four distance measurements, and four dbh measurements were recorded at each point along the transect. Also at each point, we measured the maximum horizontal spread of the nearest oak, and the spread at 90 degrees perpendicular to this maximum. The average of these two measurements was used to calculate canopy cover, expressed in m^2 per ha. The absolute density of oaks was calculated as $10{,}000/D^2$ where D=the mean distance between each sample point and its nearest oak (Mueller-Dubois and Ellenberg 1974). Percent survival was calculated as the planting density in 2001 divided by the initial planting density of acorns. Dominance of oaks was calculated as (π x [mean dbh/2]^2 x density), and is presented in cm^2 of horizontal stem-area at breast height per ha.

We used simple linear regression techniques (SYSTAT 1997) to test for possible relationships among parameters at the six sites.[4]

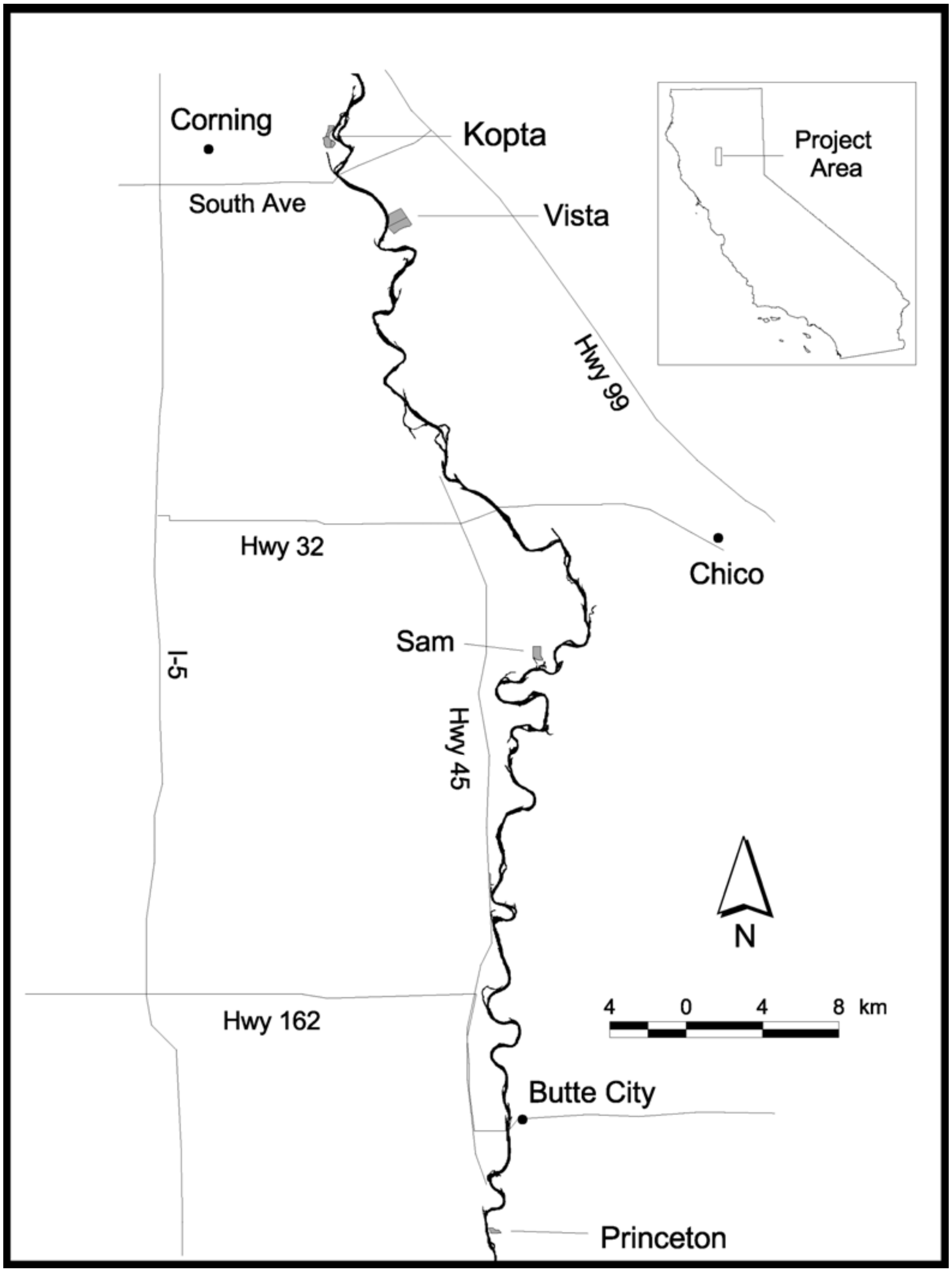

Figure 1—Location of restoration sites along the Sacramento River.

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[4] Mention of trade names or products is for information only and does not imply endorsement by the U.S. Department of Agriculture.

Results

Table 2 presents a comparison of characteristics of valley oaks at the six study sites. Overall we found that individual trees had grown quite well despite being completely unattended for the past four to seven years. We did, however, find considerable inter- and intra-site variability that is likely attributable to differences in local (and landscape-scale) physical and biological site conditions. Identifying the causes of this variability in response was beyond the scope of the current study, however.

Table 2—*Characteristics of Valley Oaks in riparian restoration units on the Sacramento River, California. Standard deviation is in parentheses.*

Site	Sampling points	Planting density (acorns per ha)	Density in 2001 (per ha)	Percent survival (per ha)	Canopy cover (m^2 per ha)	Mean dbh (mm)	Dominance (cm^2 stem area at breast height per ha)
Princeton	30	581	356	0.61	761	42.4 (38.7)	13,420
Sam	32	1,500	576	0.38	2,392	81.8 (51.2)	38,070
Vista 1	10	390	57	0.15	487	71.5 (72.1)	4,514
Vista 2	20	390	70	0.18	696	76.8 (33.8)	3,830
Kopta 2	12	500	230	0.46	211	38 (47)	3,093
Kopta 3	18	500	85	0.17	708	88.5 (47.9)	8,486

The density with which oaks were planted appears to have had a large positive effect on their density in 2001 (n=6 sites, r^2=0.81, p=0.015). The dbh of individual trees measured in 2001 did not, however, appear to be related to either planting density (n=6 sites, r^2=0.07, p=0.62) or density in 2001 (n=6 sites, r^2=0.81, p=0.015). Strong positive associations were found between original planting density and both canopy cover (n=6 sites, r^2=0.92, p=0.003) and dominance (n=6 sites, r^2=0.96, p<0.001) measured in 2001. The growth performance of individual trees appeared to be somewhat variable among sites, and highly variable within them (see standard deviation associated with dbh in *table 2*).

Discussion

Many of the valley oaks that were planted as acorns 7 to 11 years ago have developed into robust individuals that appear well on their way to forming mature trees. Valley oaks are important members of the riparian vegetation communities along lowland rivers of the Great Central Valley of California (Pavlik and others 2000), and an increase in their distribution and abundance is expected to provide numerous ecosystem benefits. It is important that the success of these efforts be documented as horticultural restoration efforts in riparian zones of the semi-arid west have not always been successful. For example, a mass die-off Fremont cottonwood in Arizona was observed several years after planting (Patten, personal communication).

Although we can not be certain that the sites surveyed in this study will have oaks that continue to thrive in the decades to come, we expect that this will be the case as the present status of these trees at many locations appears to be excellent.

Our results also suggest that there is considerable variability in the survival and growth patterns at the different restoration sites and that this is a function of both biological and physical factors. Our study thus provides preliminary information on some of the responses that may be expected when planted valley oaks adapt to the varied site conditions found on the Sacramento River floodplain.

The Sam site supported by far the greatest valley oak density, canopy cover, and dominance of any of the sites *(table 2)*. By contrast, the majority of the Kopta 2 site supported valley oak individuals that had not reached breast height after 11 years of growth. The most likely explanation for this difference is the soil characteristics of the two sites. At the Sam site the entire 28 ha is composed of a non-stratified heavy silt loam that extends downward 12 feet to the water table, while the majority of Kopta 2 site is a very sandy soil underlain by coarse sand and gravel (Alpert and others 1999). Preliminary soils data suggest that pockets of the Kopta 2 site that are composed of deep, non-stratified fine sandy loam support individual valley oaks as large as those observed on any other site. Our calculations suggest that 230 valley oaks per ha are present at Kopta 2, although many are severely stunted and few are likely to become large trees.

The Vista 1 and 2 sites have the lowest density of oaks today because of the very high mortality caused by pocket gopher populations at the time of project initiation. Most acorns and seedlings in Vista 1 and Vista 2 were consumed by the gophers in 1993 and 1994 (Griggs, personal observation). However, in early 1995 Vista experienced a flood that drowned vast numbers of gophers, voles, and ground squirrels. Not surprisingly, following the flood, valley oaks at Vista exhibited increased survival rates (Griggs, personal observation).

The variation in survival and growth of valley oaks observed within and among sites may be viewed as a favorable outcome from a restoration management standpoint. This variability in response does much to create a diverse mosaic of vegetation along the Sacramento River that can support the varied needs of the native wildlife species found in this region.

While the results of this study confirm that horticultural practices provide an effective tool in the restoration of riparian oak forests, many uncertainties remain. In particular we need to better understand how best to balance efforts directed at planting and maintaining woody overstory species with those focusing on restoring a native herbaceous understory. The importance of understory vegetation is evident from studies of songbirds conducted on restoration sites along the Sacramento River. Although Small and others (2000) found that in general, riparian breeding bird diversity increased as restoration sites matured, the degree to which individual sites were utilized by the avian community depended largely upon the understory component. Also, as alluded to earlier, restoration efforts on the Sacramento River floodplain will not be successful unless important attributes of the natural flow regime are restored. Without restoring the key components of the natural disturbance regime with which native species of this region evolved, we cannot expect to meet the complex and varied life history requirements of the rich array of organisms that this system is capable of supporting. Although gaining a sufficient understanding of ecosystem function to inform management decisions on the Sacramento River is a daunting task, initial steps are being taken to develop multidisciplinary studies of the type needed to inform this process (see Golet and others [In press] for descriptions of some of these efforts).

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Soil Moisture Availability as a Factor Affecting Valley Oak (*Quercus lobata* Neé) Seedling Establishment and Survival in a Riparian Habitat, Cosumnes River Preserve, Sacramento County, California[1]

Virginia C. Meyer[2]

Abstract

The lack of valley oak (*Quercus lobata* Neé) regeneration throughout much of its historical range appears to be related to both habitat destruction and soil moisture availability. The water relations, growth and survival of greenhouse potted seedlings, field-planted and natural seedlings were monitored through the growing season, 1989. The age structure of the valley oak population of a riparian forest at the Cosumnes River Preserve was determined. The history of fluvial events of the Cosumnes River was ascertained to determine whether such fluvial events are associated with past seedling establishment within the forest. Natural and non-irrigated field-planted seedlings exhibited considerable water stress, little stem growth and leaf loss, while greenhouse potted and irrigated field-planted seedlings displayed limited water stress. Irrigated field-planted seedlings grew vigorously. Past seedling establishment within the forest showed a positive relationship with historical fluvial events. These studies suggest that soil moisture availability is fundamentally important for successful establishment of valley oak seedlings. Significant recruitment of valley oak seedlings may be limited to years in which plentiful soil moisture is available into the growing season, i.e. with the natural flooding of unconfined riparian systems.

Introduction

The California endemic valley oak (*Quercus lobata* Neé) is found as a dominant species in riparian forests. Valley oak forests, woodlands and savanna are found on higher portions of the floodplain above riparian forests dominated by Fremont cottonwood (*Populus fremontii*) (Holstein 1984). The present extent of Great Valley riparian forests is only a remnant of what existed in the “pristine” valley. Because of the very rapid destruction of these forests, their original extent is very difficult to determine. Katibah (1984) estimated that 21,449 hectares of mature riparian forest is left in the Great Valley, most of which has been disturbed. The Cosumnes River Preserve encompasses one of the healthiest and most extensive remnants of mature valley oak riparian forest (Griggs 1987).

In addition to the loss of valley oak forests, woodlands, savannas and individuals, natural regeneration of the valley oak has been observed to be poor

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[1] An abbreviated version of this paper was presented at the Fifth Symposium on Oak Woodlands: Oaks in California’s Changing Landscape, October 22-25, 2001, San Diego, California.

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(Callizo 1983; Cavagnaro 1974; Griffin 1971, 1973a, 1976, 1977, 1980; Jepson 1910; Kirn 1982; McClaran 1983; Rossi 1980; Steinhart 1978; Stern 1977). This has prompted research on the factors considered to limit the successful establishment of seedlings. The effect of varying water regimes on growth and survival has been studied (McCreary 1989, Reynolds 1991), as have the water relations of mature trees at varying distances from a known water source (Griffin 1973b).

Since the first discovery of the valley oak, the abundance of growth of valley oaks associated with riparian forests, higher portions of floodplains, natural levees, well-watered valleys and other sites with high soil moisture availability or relatively high water tables has been reported (Canon 1914, Jepson 1910, Thompson 1961). Also reported is the demise of great numbers of valley oaks due to the pumping of ground water, water diversions, dams and flood control projects (Griggs 1990, Steinhart 1978). Studies focusing on the effects of water stress on valley oaks have been limited.

Knowledge of how water availability affects present seedlings and affected valley oak seedling establishment in the past will help to elucidate how limited water availability may be contributing to limited valley oak regeneration in California. Two main objectives were the subject of this research: 1) To determine and evaluate the water relations of greenhouse potted, field planted, and natural seedlings under differing water regimes to reveal the physiologic and growth responses of valley oak seedlings to water stress; and 2) To determine an age structure of the valley oaks in the eastern, relatively undisturbed riparian valley oak forest ("Tall Forest") at the Cosumnes River Preserve, and to determine if past seedling establishment is associated with historical fluvial events.

Methods

Study Area

The Cosumnes River Preserve is located in the central portion of California's Great Valley. The Cosumnes River flows through the Preserve and joins the Mokelumne River at the southwestern corner of the Preserve. The Cosumnes remains a major natural river system with regular flooding beyond its banks (Jones and Stokes 1974, US Army Corps of Engineers 1965). The Cosumnes River, sloughs, and backwaters of the Preserve are all affected by tidal activity. With the elevation of the land at the Preserve averaging less the 10 ft above sea level, this activity combined with high flows of the Cosumnes, ensures regular flooding at the Preserve.

Water Relations

In order to find the degree to which valley oak seedlings are dependent on the availability of soil moisture for establishment and growth in their first season, the effects of water stress on their physiology and growth was examined.

A greenhouse potted seedling study was conducted. Germinated acorns were planted in 300 1 gal plastic pots in January, 1989. The planted pots were randomly assigned to one of two groups: 1) "well-watered" group, watered every other day to saturation; and 2) "stressed" group, watered every four days to saturation. The pots were watered with a drip irrigation system.

The field-planted seedling study was conducted in the "savanna-ranch" area of the Cosumnes River Preserve adjacent to a slough. The germinated acorns were planted in January, 1989, in rows, each seed 1 ft from the next with 2 ft between rows. Three plots of five rows each with 30 seeds in each row were planted. Rigid plastic mesh seedling protection tubes were placed over each seed. The exclosure was fenced with hog wire fencing and chicken wire buried at the base of the hog wire. Field-planted seedlings were watered with a drip irrigation system with water pumped from the adjacent slough. The first plot of 150 sites, "Plot A," was watered for ½ hr twice per month from April, 1989 through August. The second plot, "Plot B," was watered for ½ hr once per month from April through August. The last plot, "Plot C," was given no supplemental water.

A population of naturally occurring seedlings growing in a young stand of valley oak in the forest of the Preserve was identified. Fifty seedlings from this population were tagged for growth measurements. Seedlings used for xylem potential and leaf conductance measurements were taken at random.

Seedlings were monitored for xylem potential and leaf conductance diurnally through the growing season (April through August) of 1989. Xylem potential was measured with a pressure bomb (Scholander and others 1965). Pressure-volume curves for the determination of osmotic potential were constructed from measurements at the end of the season in August 1989. Pressure-volume curves were constructed from measurements as per Tyree and Hammel (1972). The measurement of leaf conductance was made with the use of a stomatal diffusion porometer (Kanematsu and others 1969).

Seedling growth measurements were also made through the growing season of 1989. Leaf number increase/month and stem height added/month (cm) were recorded for all three studies. Total leaf area and root/shoot ratio measurements were made in August for the potted greenhouse seedlings. Seedlings were removed from the pots and leaves removed for leaf area measurements. Leaf area was determined by optical planimeter and root/shoot ratios were determined by measuring the dry mass of the roots and shoots.

Valley Oak Age Structure

The age structure of the valley oak trees of the Preserve's eastern riparian "Tall Forest," 45.5 hectares in extent, was determined by ring-counts of cores taken from the trees. Using an aerial photograph, the forest area was broken down into major visually distinct types, or strata, so that the valley oak population of the forest could be inventoried with a stratified random sample (Freeze 1962). The strata were further subdivided into substrata depending on location within the forest area (*fig. 1*). Plots, 809.4 square meters in size and comprising 10 percent of the total forest area that was studied, were randomly selected within each substratum by the proportional allocation method (Freeze 1962). One valley oak tree from each quadrant of each plot was cored at 1 ft above ground with an increment borer, except in substratum B1 Plots 1 and 2 and substratum C1 Plot 1 wherein all valley oak trees were cored. As annual rings of each core were counted, the boundaries between annual rings were determined using criteria described for Engelman oak (*Quercus engelmannii*) by Lathrop and Arct (1987).

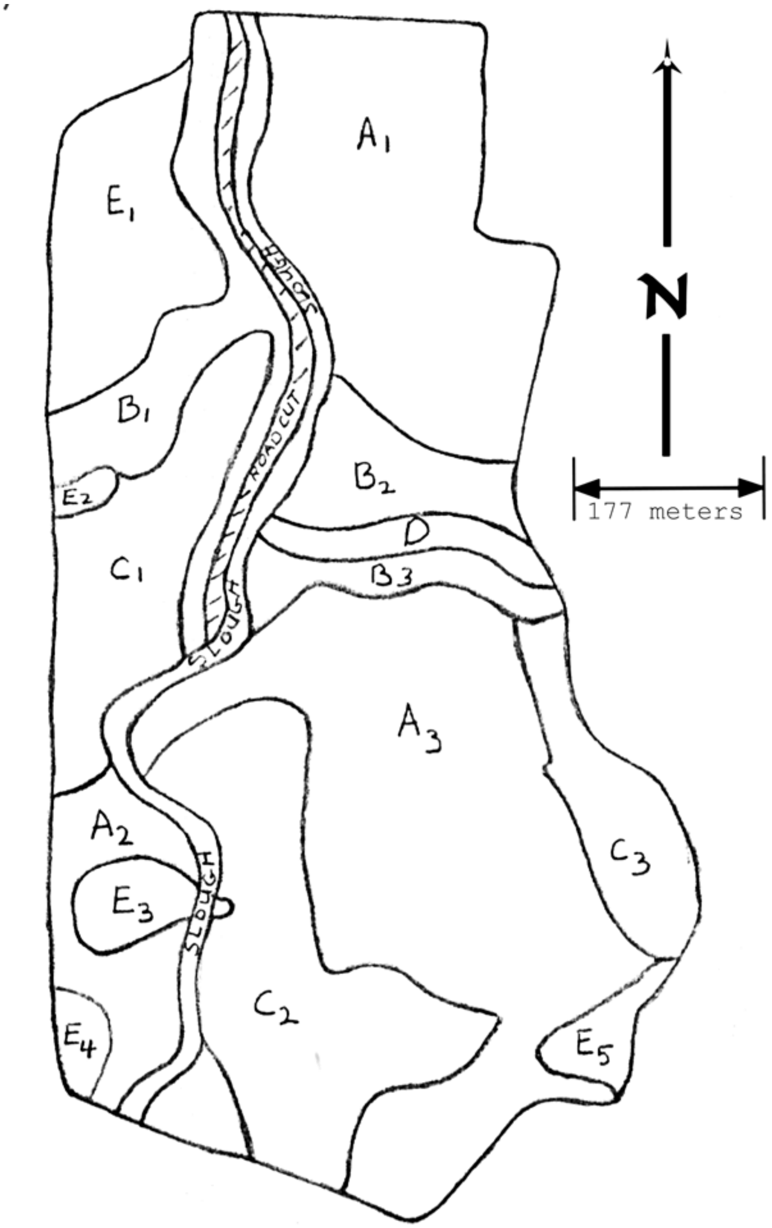

Figure 1—Map of the "Tall Trees" forest at the Cosumnes River Preserve, divided into visually distinct strata for sampling. A: tall forest, with mixed riparian trees, B: young, monospecific valley oak forest and woodland, C: forest of mostly valley oak with Oregon ash and cottonwood, D: ditch and willow thicket, E: open, with scattered old valley oak.

For fluvial event dating on the Cosumnes River, discharge records were obtained from the U.S. Geological Survey Water Resources Division for the Michigan Bar gauging station, approximately 30 mi upstream from the Preserve.

The number of trees established each year from 1915 through 1973 was graphed with discharge parameters as recorded at the Michigan Bar gauging station. The establishment year for each tree was estimated as 1989 minus the ring-count of the core sample minus 1 yr. A comparison was made between the proportion of trees established within 1 yr after a flood event (>800 cfs mean annual discharge) and the proportion of years-within-1-yr-after-a-flood event. The frequency distributions of the ages of trees sampled for ring-counts were analyzed by stem-and-leaf plots for the forest as a whole and for each of the strata (Velleman and Hoagland 1981).

Results

Water Relations

In the greenhouse study, no significant difference in mean xylem potentials or osmotic potentials was found between well-watered and stressed potted seedlings (*table 1*). The xylem potential in both treatments decreased significantly at mid-day only in August, and both treatment groups were able to recover overnight xylem potential to high pre-dawn means (*table 2*). The mean leaf conductance of the well-watered seedlings was significantly higher than that of the stressed seedlings (*table 1*). For both treatments, daily mean leaf conductances decreased through the season (*table 3*). By August, the well-watered seedlings were slightly but significantly taller, had more total leaf area and smaller root/shoot ratio than the stressed seedlings (*table 4*). Thus, the stressed seedlings reacted to the water stress by adding more root mass rather than above-ground growth.

In the field-planted seedling study, the mean xylem potentials in Plots A and B were not significantly different for the season overall, but the xylem potential of Plot C seedlings, which received no supplemental watering, was much lower than those of the seedlings in the other two plots (*table 1*). Plot C seedlings experienced a significant amount of water stress, with increasingly lower xylem potentials as the season progressed (*table 2*). The pre-dawn xylem potential of Plot C seedlings was very low (-2.08 Mpa) by the end of the season, that is, they showed no overnight recovery. There were no significant differences found between the three groups of seedlings in osmotic potential (*table 1*). Leaf conductance was highest in Plot A and lowest in Plot C for the season overall, and the leaf conductance continually decreased in Plot C seedlings over the course of the season (*table 3*). By season's end in August the mean total leaf number and stem height were also much lower in Plot C seedlings, and experienced a 9 percent mortality compared with a 4 percent mortality of Plot B seedlings and no mortality of Plot A seedlings (*table 4, fig. 2*).

Table 1—*Mean conductances, xylem potentials and osmotic potentials of greenhouse potted, field-planted, and natural valley oak seedlings for growing season, 1989.*

Seedlings	**Conductance** (cm/s)	**Xylem potential** (MPa)	**Osmotic potential** (MPa)
Greenhouse potted			
Well-watered	0.24[1]	-0.68	-1.96
Stressed	0.21[1]	-0.74	-1.52
Field-planted			
Plot A	0.21	-1.56	-1.16
Plot B	0.20[1]	-1.63[1]	-1.53
Plot C	0.16[1]	-2.40[1]	-1.46
Natural	0.15	-1.81	-1.48

[1] Denotes a significant difference down columns at $P<0.05$.

Table 2—*Mean xylem potentials (MPa) of greenhouse potted, field-planted and natural seedlings, 1989.*

		Seedlings:					
		Greenhouse		Field-planted			
Month	**Time**	**Well-watered**	**Stressed**	**Plot A**	**Plot B**	**Plot C**	**Natural**
April	0400	-0.43	-0.24	------	------	------	-0.48
	1200	-0.88	-0.79	------	------	------	-1.64
May	0400	-0.22	-0.32	-0.41	-0.44	-0.49	-0.71
	1200	-1.13	-1.00	-2.02	-2.34	-2.78	-2.18
June (E)	0400	-0.33	-0.16	------	------	------	-0.62
	1200	-0.57	-0.86	------	------	------	-1.84
June(L)	0400	-0.22	-0.24	-0.44[2]	-0.55[2]	-1.56[2]	-1.20
	1200	-0.85	-1.17	-3.03[2]	-1.23[2]	-2.10[2]	-1.34
July	0400	-0.33	-0.30	-0.42[2]	-0.57[2]	-1.86[2]	-2.34
	1200	-0.58[1]	-1.30[1]	-2.22[2]	-2.61[2]	-4.14[2]	-2.50
August	0400	-0.34	-0.35	-0.22[2]	-0.26[2]	-2.08[2]	-2.95
	1200	-2.32	-2.47	-1.55	-2.12	-2.66	-3.39

[1] Denotes a significant difference between means of groups of greenhouse study at P<0.05.

[2] Denotes a significant difference between means of groups of field-planted study at P<0.05.

Table 3—*Mean leaf conductances (cm/s) of greenhouse potted, field-planted and natural seedlings, 1989.*

	Seedlings:					
	Greenhouse		Field-planted			
Month	**Well-watered**	**Stressed**	**Plot A**	**Plot B**	**Plot C**	**Natural**
April	0.36[1]	0.31[1]	-------	------	-------	0.28
May	0.30	0.26	0.24[2]	0.18[2]	0.21	0.18
June (E)	0.22	0.23	-------	------	------	0.21
June (L)	0.22[1]	0.17[1]	0.22[2]	0.22[2]	0.16[2]	0.10
July	0.20[1]	0.14[1]	0.20[2]	0.19	0.15[2]	0.08
August	0.16	0.14	0.20[2]	0.20[2]	0.14[2]	0.07

[1] Denotes a significant difference between means of groups greenhouse study at P<0.05.

[2] Denotes a significant difference between means of groups of field-planted study at P<0.05

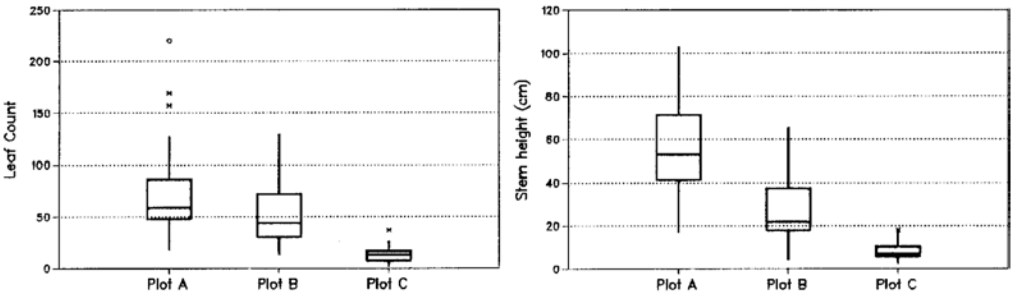

Figure 2—Leaf count and stem height distributions of field-planted valley oak seedlings in August 1989, Cosumnes River Preserve. Horizontal bars indicate median; vertical bars indicate range; * and o denote outliers.

Table 4—*Mean growth (total leaf number, total stem height, leaf area, and root/shoot) and growth rates (leaf number added/month and stem height added/month) of greenhouse potted seedlings, field-planted seedlings and natural seedlings, 1989.*

	Seedlings:					
	Greenhouse		Field-planted			
Month	**Well-watered**	**Stressed**	**Plot A**	**Plot B**	**Plot C**	**Natural**
Total leaf #	11[1]	8[1]	72[2]	52[2]	13[2]	------
Total stem height (cm)	14.0[1]	10.0[1]	56.5[2]	27.5[2]	8.0[2]	------
Leaf area (cm^2)	9.06[1]	6.73[1]	------	------	------	------
Root/shoot	7.28[1]	9.85[1]	------	------	------	------
Leaf added per month	2	1	14[2]	11[2]	3[2]	2
Stem height added per month	2.5	1.5	11.5[2]	5.5[2]	1.5[2]	1.2

[1] Denotes a significant difference between means of groups of greenhouse study at P<0.05.

[2] Denotes a significant difference between means of groups of field-planted study at P<0.05.

The natural seedlings, as with the unwatered field-plot seedlings, had increasingly lower xylem potential as the season progressed, with July and August pre-dawn xylem potentials approaching the mid-day values (*table 2*). The osmotic potential of August was similar to that found in the other studies. Leaf conductances of the natural seedlings decreased over the course of the season also, with a slight recovery in early June after a June 4 thunderstorm (*table 3*). The natural seedlings tagged for growth measurements averaged 2 yrs in age. In April the tagged seedlings had a mean of 10 leaves and were an average of 21.5 cm in height. By August there was a net increase of one leaf per seedling and an increase in stem height of 5.5 cm (*table 4*).

By examining all three studies together, patterns of stress emerge. High pre-dawn xylem potentials were maintained throughout the season by the greenhouse and Plots A and B seedlings, while the pre-dawn xylem potentials gradually decreased in Plot C and the natural seedlings. Both the unwatered Plot C field-planted seedlings and the natural seedlings were under continuing water stress as the season progressed. The greenhouse, Plot C and natural seedlings all displayed a continuing decrease in conductance as the season progressed as well. Plot C and natural seedlings experienced “flatter” diurnal curves of conductance in August, but even this response did not enable these seedlings to recover xylem potential; they were unable to draw enough water from the soil. The greatest growth rates were recorded for the field-planted Plots A and B seedlings. Plot C and natural seedlings all showed very little growth from April through August.

Valley Oak Age Structure

The forest area is bounded by the Cosumnes River at the south, a previously agricultural field to the west and north, and an agricultural field to the east. A slough traverses through the forest from the river. As described above, the forest was broken down into five major strata of visually distinct types and substrata using an aerial photograph (*fig. 1*). Stratum A is tall forest of mixed riparian species. Stratum B is woodland, with almost exclusively young valley oak. Stratum C is forest of mostly valley oak). Stratum D is a single strip along a branch the slough apparently completely cleared and now consisting of willow-scrub. Stratum E represents the areas of the forest that are presently open, apparently cleared and now are composed of annuals, grasses and scattered saplings of valley oak and very old, remnant valley oak trees.

From the graphs of the number of trees established in each year and the discharge parameters, a tendency for more trees to become established in years with a higher discharge can be discerned (*fig. 3*), especially in the years 1952 and 1956. In contrast, fewer trees became established in years with low discharge. The comparison between the proportion of trees established within one year after a flood event of >800 cfs mean annual discharge and the proportion of years-within-one-year-after-a-flood event revealed a significant difference for the forest as a whole and for Stratum B (*table 5*).

Stem-and-leaf analysis of the ring-counts of all 155 trees sampled for core age in the forest shows 52 percent of the counts between 30 and 49 years (*table 6*). Trees samples in Stratum A were medium-aged, with a mean of 46 years, those of Stratum B were youngest with a mean of 32 years, and the trees of Stratum C were oldest with a mean of 50 years (*table 7*).

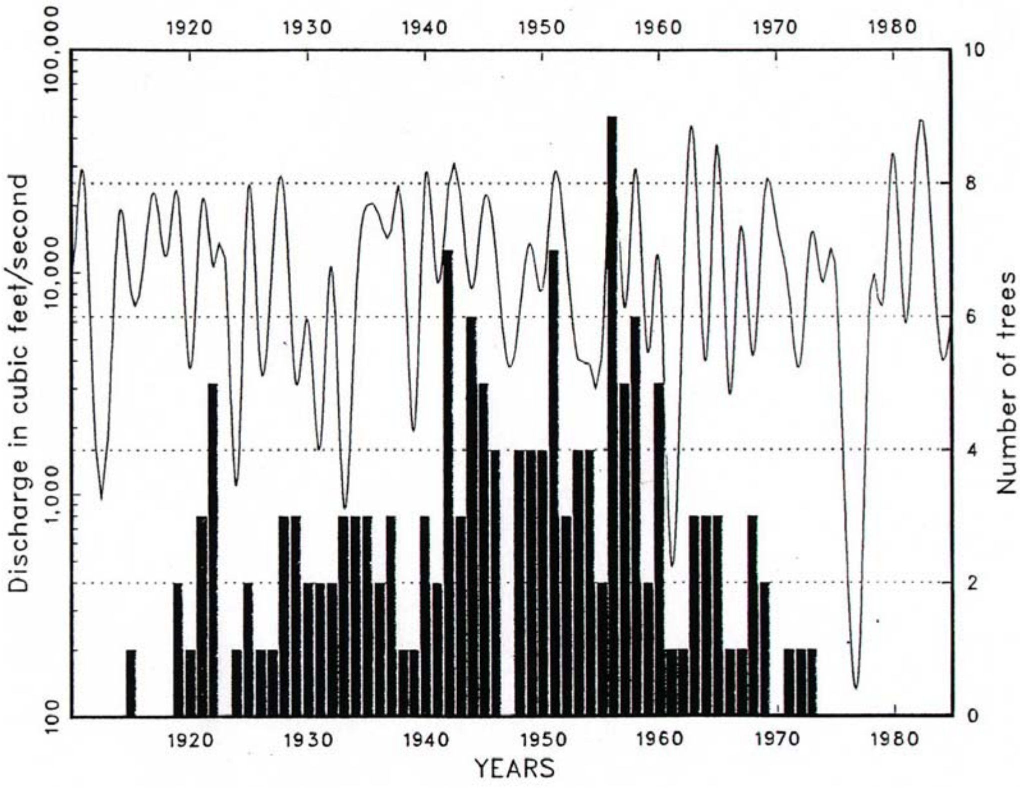

Figure 3—Number of valley oak trees established each year in the “Tall Trees” forest at the Cosumnes River Preserve, and the peak discharge (cubic ft/sec, cfs) recorded each year at US Geological Survey Michigan Bar gauging station, 1910-1985.

Table 5—*Comparison of the proportion of trees established in the "Tall Trees" forest at the Cosumnes River Preserve, within one year after a flood (>800 cfs mean annual discharge) and the proportion of years-within-a-year-after-a-flood, as recorded at the USGS Michigan Bar gauging station on the Cosumnes River.*

	Total years	**Trees**		**Years**	
		n	**pct within 1 yr**	**n**	**pct within 1 yr**
Forest	1915-73	155	22[1]	59	15[1]
Stratum					
A	1921-65	35	14	45	16
B	1931-73	63	36[1]	43	21[1]
C	1915-69	55	13	55	16

[1] Denotes a significant difference across rows at P>0.05.

Table 6—*Stem-and-leaf[1] age distribution of the population of valley oaks of the "Tall Trees" forest at the Cosumnes River Preserve, 1989.*

Forest
n = 155
Leaf Unit = 1.0 year

5	1	56799
16	2	00012333444
29	2	5556778888899
54	3	0000001111122222222334444
76	3	5555666777777888899999
(19)	4	0000222233333444444
60	4	555666666677888
45	5	011122333444
33	5	555667788999
21	6	000112334
12	6	66666777899
1	7	3

Stratum A
n = 35
Leaf Unit = 1.0 year

2	2	34
4	2	57
5	3	4
11	3	567789
16	4	02344
(4)	4	5678
15	5	2344
10	5	555688
4	6	01
2	6	77

Stratum B
n = 63
Leaf Unit = 1.0 year

3	1	569
11	2	00012344
20	2	556788899
(21)	3	000000111122222223344
22	3	55677788999
11	4	2234
7	4	668
4	5	01
2	5	57

Stratum C
n = 55
Leaf Unit = 1.0 year

1	1	9
2	2	3
3	2	8
6	3	124
11	3	56789
21	4	0002333444
(8)	4	55666678
22	5	67999
17	6	0012334
10	6	666667899
1	7	3

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[1] Left column of each display is depth of leaf, or count at each stem; center column is stem of plot, i.e. the first digit of each value of the ring count; right column is leaf of plot, or second digit of each value of the ring count of same stem, e.g. 56799 leaf of stem 1 arranges values of 15, 16, 17, 19 and 19 ring counts. The parenthesis in the first column denotes the leaf with the median value of the ring count of the plot.

Table 7—*Age structure of sampled valley oak trees of the "Tall Trees" forest at the Cosumnes River Preserve, and of each of the strata of the forest, 1989 (n= number).*

	Age	
	mean	**n**
Forest Stratum	42	155
A	46	35
B	32	63
C	50	55
E	32	3

Discussion and Conclusions

Water Relations

Evidence of considerable water stress was found in both unwatered first-season field-planted seedlings and in natural valley oak seedlings growing in the forest of the Preserve. Since neither of these groups received irrigation, the stress evidenced in water relations measurements and in the very slight growth during the growing season may represent stress of natural seedlings under canopy cover and in the open.

Osmotic potentials between groups of greenhouse and field-planted seedlings suggest no osmotic adjustment, that is, no decrease in cell osmotic potential for intake of water by passive diffusion. Unlike valley oak, blue oak seedlings show decreased osmotic potentials through the growing season with osmotic adjustment and this was important for seedling survival (Menke, no date; Momen and others 1994). If osmotic adjustment does not occur in water-stressed valley oak seedlings, their ability to deal with water stress successfully would be limited.

Most striking is the abundant growth of the field-planted seedlings that were irrigated in Plots A and B. Greenhouse, natural and non-irrigated Plot C seedlings all grew very little during the season. Non-irrigated Plot C seedlings had the advantages of the other field-planted seedlings (unencumbered root growth and lack of competition), but still did not grow significantly more or faster than the natural seedlings. This suggests that these advantages can be translated into increased growth rates only when sufficient soil moisture is available. Cell growth has been shown to be very sensitive to water stress, more sensitive than either stomatal opening or carbon assimilation (Salisbury and Ross 1985). Thus, growth is affected by water stress before transpiration is decreased. Valley oak seedlings may be more limited than the seedlings of other California oaks in their ability to survive and grow during the summer drought. As a deciduous oak with thin leaf cuticle, valley oak continues to lose water through cuticular transpiration after stomata are completely closed (Rundel 1987). Though valley oak seedling roots grow quickly, they lack the drought-resistant characteristics of other deciduous oaks, such as blue oak.

Age Structure

The positive relationship between years of high mean annual discharge and valley oak tree establishment supports the conclusion reached in the population structure study conducted at the Bobelaine Sanctuary on the Feather River: more valley oak seedlings and saplings survived in more mesic habitats (Knudsen 1987). The increased tendency for tree establishment to occur in years of high mean annual discharge was most pronounced in Stratum B of the forest at the Preserve. This area of the forest had been without tree cover since 1937. The canopy of this substratum is comprised almost entirely of valley oak trees. From the age distribution (Table 5), it is seen that the valley oak stand of Stratum B was more even-aged that the stands of the other forested strata. The composition of the other forested areas (Strata A and C) is of mixed trees, including obligate phreatophytes such as Fremont cottonwood and willows (Barbour 1987). From this composition, it may be presumed that the land of these strata was more frequently inundated by flood waters and that the establishment of valley oak would be less dependent upon unusual fluvial events within these strata. In fact, the ages of the valley oak trees in these strata were mixed. In Stratum B, the establishment of the more even-aged stand of valley oak appears to have been facilitated by the high flows of the Cosumnes River in the 1950's and inundation by flood waters. Stratum B is located farther from the river than the strata with mixed riparian species. This distribution fits the patterns described by previous studies (Barbour 1987, Conard and others 1980, Holland and Roye 1989, Holstein 1984, McBride and Strahan 1984, Strahan 1984).

The stem-and-leaf plot analysis of the age distribution for the trees sampled in the forest as a whole shows the highest number of ages in the mid-range, 30 to 50 years *(table 6,* Forest). The age distribution for the trees of Stratum B is bell-shaped, whereas the distributions for the trees of Strata A and C are bimodal. Of the ages obtained, in the trees of the strata separately and as a whole, there is a tapering off in the number of trees in the younger age classes. This suggests that conditions optimal for valley oak establishment were present in each of the strata for a number of years and that subsequent establishment was suppressed or that the younger age-classes of trees were more susceptible to mortality. Thus, the age distributions of the different strata of the forest suggest that the establishment of valley oak in the forest tends to be episodic and not continuous.

The natural flooding events at the Preserve which were correlated with increased establishment of the valley oak in the forest may have also drowned small mammals that "are the major predators on acorns and oak seedlings" (Griggs 1990). The herbivory by small mammals, especially pocket gophers, has been implicated as a limiting factor of native oak seedling establishment in many studies (Adams and others 1987; Borchert and others 1989; Griffin 1971, 1973, 1976, 1980; Knudsen 1987). Thus, the natural flooding processes of unconfined river systems may provide a combination of reduced acorn and seedling predation and high soil moisture levels into the growing season during high water years. This combination of factors may be necessary for successful valley oak establishment in areas not inundated on a yearly basis. Alternatively, high soil moisture may allow valley oak seedlings to grow at a rate fast enough that such seedling herbivory that did occur would not have as devastating an impact on overall seedling survival and establishment.

Conclusion

A number of problems exist in interpreting native California oak regeneration, including a dearth of documentation of past distribution and stand structure (Bartolome and others 1987). Because of the plethora of factors that may be causing the present patterns of seedling and sapling recruitment, and because these factors vary considerably in space and time, Muick and Bartolome (1987) considered these present patterns to be "highly species and site-specific." The pattern of more frequent recruitment and successful establishment of valley oak in more mesic sites and lower sites has been observed in previous studies (Knudsen 1987, McBride and Strahan 1984, Strahan 1984). The water relations findings of the present studies provide evidence that variations in soil moisture availability are a major factor in explaining this pattern.

The regeneration of riparian valley oak forests is dependent on the natural flooding processes of unconfined river systems. The periodic intense and sustained inundation almost certainly provides high soil moisture levels into the growing season and either drowns small mammal herbivores or provides sufficient moisture to allow fast enough growth rates to avoid devastating effects of herbivory.

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Factors Limiting Recruitment in Valley and Coast Live Oak[1]

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Abstract

The Santa Barbara County Oak Restoration Program was initiated in 1994 to determine the major factors limiting recruitment of valley oak (*Quercus lobata*) and coast live oak (*Q. agrifolia*). At Sedgwick Reserve in Santa Barbara County, California, we have replicated large-scale planting experiments in four different years to determine the effects of cattle and other ecological factors on oak seedling establishment in oak savannas and woodlands. In 33 large experimental plots (50 x 50 m) we planted acorns collected from *Q. lobata* and *Q. agrifolia* on the site. Fifteen of these large plots are controls, open to grazing, fifteen exclude cattle with the use of electric fence, and three are ungrazed in large ungrazed pastures. Within the plots, experimental treatments included: 1) protection from small mammals such as gophers and ground squirrels, 2) protection from large animals such as cattle, deer, and pigs, and 3) no protection from mammalian grazers. In winters 1997, 1998, 2000, and 2001, we planted approximately 1,000 acorns of each species. Results confirm that seed predation and herbivory by small mammals are a significant "bottleneck" to oak seedling recruitment on the landscape scale. Comparing results among years indicates that lack of late winter rainfall can significantly reduce oak emergence and establishment. Survivorship of protected acorns and seedlings is comparable in grazed and ungrazed areas.

Introduction

Oak woodland and savanna habitats, among the most diverse communities in North America, have suffered significant losses in the past century (Bolsinger 1988), primarily due to agricultural conversion and urban development. In addition, natural regeneration of the keystone species (in the genus *Quercus*) of these systems appears to be insufficient to maintain current populations. Many reasons for this lack of recruitment have been proposed including: 1) intense browsing of saplings and seedlings from large mammals (both deer and introduced cattle) (Griffin 1971); 2) acorn predation by cattle, deer, ground squirrels and others (up to 100 percent predation in some cases) (Borchert and others 1989); 3) trampling by cattle (Griffin 1973); 4) underground root attack from fossorial rodents (primarily gophers); 5)

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competition with exotic annual grasses for water (Danielson and Halvorson 1991); and 6) soil compaction by cattle (Braunack and Walker 1985).

More than 75 percent of oak woodland in California is grazed by cattle, making cattle the most pervasive anthropogenic influence on these ecosystems. Thus, the effects of cattle grazing must be a central theme in a comprehensive investigation of natural regeneration and restoration in today's oak savanna/woodland communities. Although cattle have been implicated as a primary cause of the failure of natural oak recruitment (Griffin 1973), their effects are clearly not straightforward. Even in areas that have not been grazed by cattle for almost 60 years (e.g., the U.C. Hastings Reserve), there is still a lack of significant oak regeneration.

The Santa Barbara County Oak Restoration Program was initiated in 1994 with the goals of determining the major factors limiting recruitment by valley oak (*Quercus lobata*), and coast live oak (*Q. agrifolia*). and identifying cost-effective techniques for large-scale oak restoration in grazed savannas. The primary foci of this program are the effects of cattle, small mammals, and interannual weather variations. Here we present preliminary results from four years of experimental plantings in this long-term oak regeneration program.

Methods

Research was conducted on the Sedgwick Reserve, a 5,883-acre (2,382-ha) ranch located in the Santa Ynez Valley in Santa Barbara County, California. The climate is Mediterranean, with hot dry summers and cool wet winters. Mean annual rainfall is 397 mm. Total precipitation (as recorded at the nearest National Weather Service recording station) for the rain years 1996-1997, 1997-1998, 1998-1999, 1999-2000, and 2000-2001 was 298 mm, 828 mm, 309 mm, 387 mm, and 649 mm, respectively. Under a cooperative grazing agreement with the College of Agriculture at California Polytechnic University, San Luis Obispo, students and faculty from Cal Poly maintained and cared for the cattle herd at Sedgwick, and assisted with the application of grazing treatments in our experiments.

Our large experimental plots were 50 x 50 m. Fifteen of these large plots were controls, open to grazing, and fifteen excluded cattle with the use of electric fence. These plots were established in 1995. They were chosen as pairs, with one randomly selected to be fenced to exclude cattle. In addition, three single 50 x 50 m plots were established in 1996 in three large ungrazed areas.

Within the plots, experimental treatments included: 1) protection from small mammals such as gophers and ground squirrels *(fig. 1a),* 2) protection from large animals such as cattle, deer, and pigs *(fig. 1b),* and 3) no protection from mammalian grazers *(fig. 1c).* Large cages were constructed of 4 ft high, 2 x 4 inches mesh galvanized wire (12 gauge); they were round (diameter = 18 inches) and supported at one side with a 5 ft t-post, and at the other side with a 4 ft rebar. Smaller cages to exclude small mammals were cylinders constructed of 3 ft high hardware cloth (mesh size = 0.5 inches); they were sealed at both ends with aviary wire. In positions with cages (small mammal exclusion), the cages were set 12 inches into the ground. Each of these treatments was replicated five times within each plot for each species.

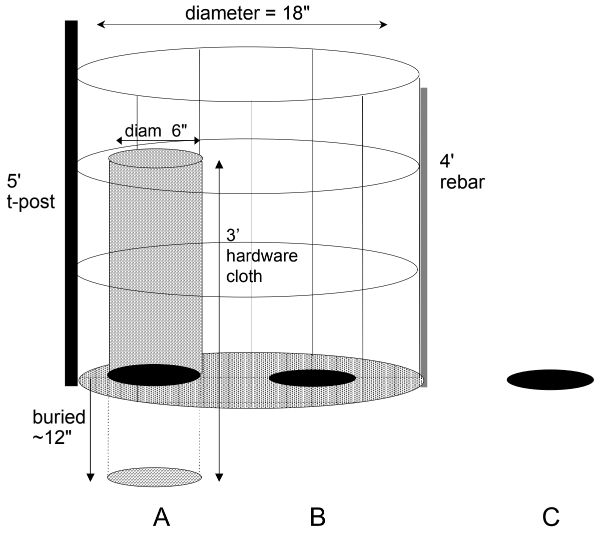

Figure 1—Treatments used for acorn plantings. A: caged and fenced to prevent grazing and herbivory by both large and small mammals (this treatment is referred to as "no rodents"). B: fenced to prevent grazing by large animals. C: open. These treatments are replicated in both 1) plots that are grazed by cattle and 2) plots that are fenced to exclude cattle.

Following the onset of consistent seasonal rains (December or January), at each planting location holes were augured to a depth of 12 inches, soil replaced and two viable acorns planted 1-2 inches below the soil surface. We planted acorns collected from *Quercus lobata* and *Q. agrifolia* on the site in the fall of the same year. Prior to planting, acorns were placed into buckets of water. Acorns that floated were discarded; we planted only acorns that sank and appeared viable. Acorns and seedlings did not receive supplemental watering through artificial irrigation.

In winters of four years, 1996-1997, 1997-1998, 1999-2000, and 2000-2001, we planted approximately 1,000 acorns of each species. In 1996-1997, and 1997-1998, we planted in all 33 plots. In January 1998 (El Niño year), the trees in the middle of two of these plots were blown over. The broken trunks and downed large limbs made future planting in these plots unfeasible. Because the plots are paired, we removed the two sets of plots (total of four) from additional planting experiments, reducing the number of plots in 1999-2000, and 2000-2001 to 29: 13 fenced, 13, unfenced, and 3 in large ungrazed pastures.

Results

2000-2001 Planting

Grouping all treatments, 17 percent of *Q. lobata* seedlings emerged, and 26 percent of *Q. agrifolia*. There were striking differences in emergence rates among experimental treatments *(fig. 2)*. The highest seedling emergence was found in locations that were protected from both rodents and large grazers. It appears that there were no differences in initial emergence rates in large grazed versus ungrazed plots, indicating that cattle grazing did not affect emergence of oak seedlings. At present, grouping all treatments, there are 405 newly emerged seedlings from the 2000-2001 plantings (160 *Q. lobata* and 245 *Q. agrifolia*).

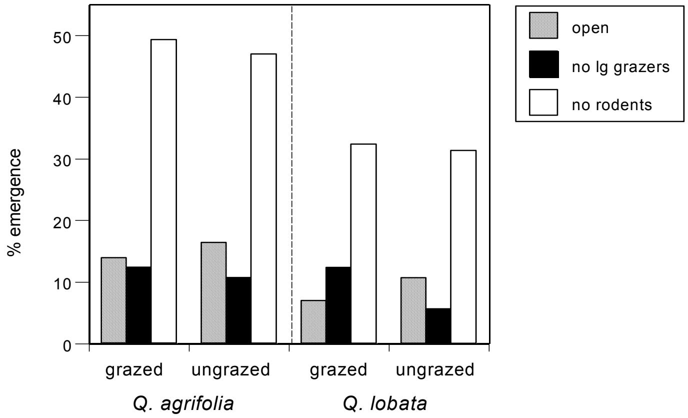

Figure 2—Total percent emergence of seedlings planted in 2000-2001 with various levels of protection from herbivores. Data are from May/June 2001.

1999-2000 Planting

The highest emergence and survivorship has been for seedlings that are protected from small mammals *(fig. 3)*. However, mortality of 1-year-old seedlings, especially *Q. agrifolia*, has occurred over the past year. It appears that there was relatively higher mortality for both species in the large ungrazed plots. In terms of actual seedling numbers, there are currently 337 established 1-year-old seedlings (273 *Q. lobata*, and 64 *Q. agrifolia*). Fifty percent of these seedlings are in the treatment protected from rodents.

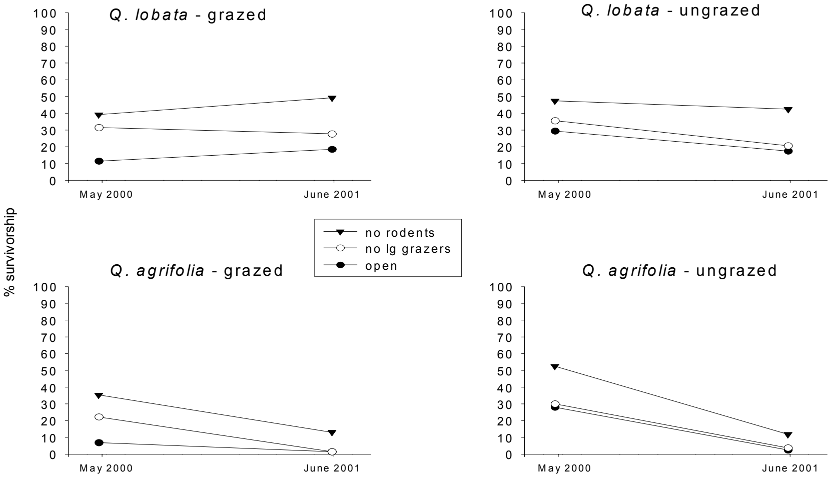

Figure 3—Percent survivorship of 1-yr-old seedlings (planted in 1999-2000) in large plots grazed by cattle, vs. those fenced to exclude cattle. Data are totals for three experimental treatments *(fig. 1)* for two sampling dates

1997-1998 Planting

The highest seedling/sapling establishment rates are for those protected from small mammals *(fig. 4)*. In nearly all treatments highest mortality thus far appears to have occurred in the first season after emergence. However, it is interesting to note that there was higher mortality for both species in the plots that have been ungrazed (see "no rodent treatment," *fig. 4)*. In terms of actual seedling numbers, there are currently 526 established three-year-old seedlings (300 *Q. lobata*, and 226 *Q. agrifolia*). Sixty-seven percent of these seedlings are in the treatment protected from rodents.

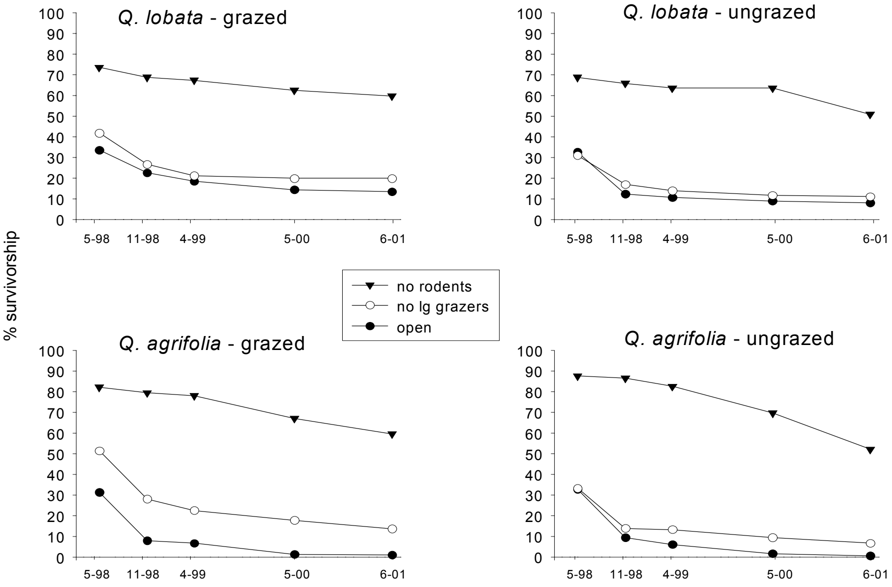

Figure 4—Percent survivorship of 3-yr-old seedlings (planted in 1997-98) in large plots grazed by cattle, vs. those fenced to exclude cattle. Data are totals for three experimental treatments *(fig. 1)* for five sampling dates.

1996-1997 Planting

Out of 2,112 acorns planted in 1996-1997, a total of 13 four-year-old established seedlings have survived, or less than 1 percent of each species planted *(table 1)*. There are presently 4 four-year old *Q. agrifolia* seedlings, and 9 four-year old *Q. lobata*. Our results suggest that the treatment that was most successful in terms of oak establishment was that which excluded small mammals. There are no seedlings surviving from the 1996-1997 planting that were in the open.

Table 1—*Percent survival of seedlings of each species in each age class to June 2001 (all treatments combined). No acorns were planted in 1998-1999 because acorns were unavailable.*

	Planting year				
	1996-1997	**1997-1998**	**1998-1999**	**1999-2000**	**2000-2001**
Quercus lobata	0.9	21.6	-	29.4	17.2
Quercus agrifolia	0.4	16.3	-	6.9	26.4
No. planted per sp	1,056	1,386		928	928

Discussion

Results from our four large-scale planting experiments indicate that several factors play a role in limiting or promoting seedling recruitment of oaks, most notably rainfall and herbivory by small mammals. Abundant rainfall in late winter, as seen in the El Niño year 1997-1998, can significantly enhance emergence and survivorship, while very low rainfall, as seen in 1996-1997, results in low seedling numbers. The effects of annual variation in precipitation levels, which are directly related to soil-moisture levels, on oak establishment have been described in previous studies. Griffin (1971) proposed that reduced rainfall greatly reduced establishment of blue and valley oak in central California. Plumb and Hannah (1991) concluded that low rainfall was the primary cause for poor success in regeneration work with coast live oak. In our study, which aims to determine cost-effective methods for oak restoration on a large landscape scale, plants have not been artificially watered because a) irrigation is expensive and may be economically infeasible on a large scale, and b) the long-term survivorship of saplings following weaning of supplemental watering is unknown. However, it is clear that adequate rainfall in the first year after planting will directly affect the success of restoration efforts.

As observed in all four planting years, at all planting sites, in both grazed and ungrazed plots, and for both oak species, seed predation and herbivory by small mammals (most likely gophers and ground squirrels, both of which are abundant at the site) significantly reduces oak seedling recruitment. The role of small mammals in oak seedling mortality has been suggested by a number of studies (e.g., Adams and others 1987, Adams and others 1997, Berhardt and Swiecki 1997, Borchert and others 1989, Davis and others 1991, Griffin 1976, McCreary and Tecklin 1997). However, in cases where seedlings are protected from herbivory with the use of window screening or tree shelters, it is difficult to separate the effects of small mammals from insects, since these treatments exclude both. The present study indicates that small mammals play a major role in limiting recruitment of valley and coast live oak.

Finally, although there appears to be no difference in initial seedling emergence in large grazed vs. ungrazed plots, our results suggest that there may be higher mortality in ungrazed plots. These latter plots, which have been ungrazed since January 1995, now have dense herbaceous vegetation. It is possible that this thick cover of thatch and grasses either 1) negatively affected the oak seedlings directly by competing for water (Gordon and Rice 1993), or 2) attracted higher densities of herbivores. We believe that the higher mortality was due to the latter, in particular herbivory by insects. This past summer (2001) we observed an outbreak of grasshoppers at our site, and many of our seedlings, in all treatments, were defoliated. Previous studies have found that reducing cover of grasses, either by weeding or grazing, significantly enhanced emergence or survivorship in oaks (Adams and others 1997, Berhardt and Swiecki 1997, McCreary and Tecklin 1997). While reduced competition was one outcome of these treatments, several studies note that weed control also reduced damage by animals that are attracted to thick herbaceous cover, such as voles (Bernhardt and Swiecki 1997) and grasshoppers (McCreary and Tecklin 1994).

Acknowledgments

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Stump Sprouting of Blue Oaks Ten Years after Harvest[1]

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Abstract

A study was conducted at five sites throughout California to determine how the sprouting of harvested blue oak (*Quercus douglasii*) is affected by the date the trees are cut down, the height of the residual stumps, and whether stumps are protected by fencing or not. After 10 years, 34 percent of the stumps had viable sprouts. The greatest effects were from fencing. Four times as many protected stumps survived than those exposed to browsing animals. Most of the mortality in unfenced areas occurred since the last evaluation eight years ago. Twice as many 90-cm-tall stumps had surviving sprouts than basal-cut stumps, and these sprouts were both taller and had larger diameters. Differences among harvest dates were relatively small, but there were significant differences among sites for most variables evaluated. However, there were no clear site attributes to explain these differences. These results indicate that the cutting of trees in densely stocked blue oak stands can be used to alter the age structure of stands and foster the establishment of young sprout-origin trees. The replacement of even-aged stands with stands of varying ages may help mitigate the negative impacts of inadequate regeneration.

Introduction

Purpose of Original Study

In 1987 a study was initiated at five sites throughout the range of blue oak in California to examine the sprouting of this species following harvest *(table 1)*. One of the objectives of this project was to identify variables that influenced sprouting so that sprouting could be encouraged in densely stocked stands that were thinned. Such thinning might be undertaken to obtain firewood, to increase forage production, or to enhance the growth of residual trees. Since it has been shown that natural regeneration of blue oak is inadequate to sustain populations in portions of the blue oak range (Bolsinger 1988, Muick and Bartolome 1987, Swiecki and others 1997), knowing which variables influence sprouting could be used to develop a harvest strategy that alters the age structure of stands through harvesting, potentially promoting stand longevity.

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[1] An abbreviated version of this paper was presented at the Fifth Symposium on Oak Woodlands: Oaks in California's Changing Landscape, October 22-25, 2001, San Diego, California.

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Table 1—*Characteristics of blue oak study sites.*[1]

	County				
Site characteristics	**Mendocino**	**Glenn**	**Butte**	**Amador**	**San Luis Obispo**
Elevation (m)	490	240	170	82	550
Density (stems/ha)	483	518	464	470	485
Basal area (m^2/ha)	17	9	15	12	11
Annual precipitation (cm)	93	55	52	46	55
Soil:					
Depth (cm)	60	70	45	100	42
Texture	silt loam	clay loam	clay loam	grav. loam	grav. loam
Series	Laughlin	Sehorn	Auburn	Red Bluff	Millsholm
Subgroup	Ultic Haploxeroll	Entic Chromoxerert	Lithic Xerochrept	Ultic Palexeralf	Lithic Xerochrept

[1] Precipitation data are from the nearest NOAA weather station. Soils information is from U.S. Soil Conservation Service reports for Glenn, Butte, Amador, San Luis Obispo and Mendocino Counties.

Methods of Original Study

The original study was designed to evaluate the sprouting of blue oak in response to season of harvest, stump height, protection from browsing animals, and stand location. The harvest sites ranged from Glenn County in the north to San Luis Obispo County in the south: three were located in the foothills of the coast range, and two in the foothills of the Sierra Nevada.

Four plots were established at each site. Each plot contained at least 96 trees with a diameter breast height (DBH) of 7 cm or larger. Plots ranged in size from 0.15 to 0.30 ha. At each site two plots were randomly chosen to be "protected", and two were left "unprotected". Protection consisted of erecting a 1.8-m tall fence around the plot perimeter, effectively preventing access by deer, cattle, and sheep. While unprotected plots at each site were grazed by domestic livestock, season of use and stocking rate were not recorded.

Within each plot trees were tagged with sequential numbers from 1 to 96. Half of the tagged trees within each plot were randomly selected for harvest. Of these 48 harvest trees per plot, 12 were harvested in each of the four seasons (summer, fall, winter and spring). Of these 12 harvest trees per plot and harvest season, half were randomly chosen to be cut at 90 cm, and half at ground line.

All plots were evaluated at the end of 1988 and 1989. Each harvested stump was evaluated for presence or absence of living sprouts, number of sprouts, length of the longest sprout, and evidence of browsing damage. Results from this trial were presented at the "Symposium on Oak Woodlands and Hardwood Rangeland Management" at Davis in 1990 (McCreary and others 1991). Results indicated that harvest date had relatively little influence on sprouting, while stump height had a large effect, with a greater percentage of taller stumps sprouting. Similarly, there were significant differences in percent sprouting and average sprout growth among sites, with the most favorable site having sprouts more than twice as long as sprouts from the least favorable site. Fencing had relatively little effect on the incidence of sprouting, but greatly influenced the lengths of longest sprouts, with fenced plots having longer sprouts. Incidence of sprouting was negatively correlated with DBH of the cut trees.

Methods

In late 1997, all plots were revisited and all stumps reevaluated. Each stump was assessed for presence or absence of living sprouts, length of the longest sprout, and diameter of the largest sprout at its base. The length of the longest (tallest) sprout was the distance from the base of the stump to the tallest point in the stump clump. We also evaluated each stump (with or without living sprouts) for deterioration and decay, assigning a score from 1 to 4, with higher values indicating more stump deterioration. Except for sprout diameter and the decay rating, these were the same variables measured in 1988 and 1989.

Data was analyzed as it was following the 1989 assessment using analysis of variance for a doubly nested randomized block design, with sites as the main plots, fences as the sub-plots, and combinations of harvest dates and stump heights as the sub-sub plots. However, due to missing data resulting from higher mortality, by 1997 a simplified model was required to analyze all variables except survival. Because few differences were found for harvest dates when this study was evaluated in 1988 and 1989, and the average height, diameter and number of sprouts were similar among the four harvest dates during the 1997 evaluation, we used a simplified model that combined responses among harvest dates. Because even a survival of zero did not result in any missing values, this variable was analyzed as before using the full model. Finally we compared decay ratings among stumps with and without surviving sprouts, and among fencing and stump heights, using two-sample t tests.

Results

Survival (Percentage of Stumps with Living Sprouts)

Overall survival dropped from 63 percent to 34 percent during the eight years between measurements. However, this reduction in survival was not equally apportioned among treatments. By far the largest reduction in survival was for unfenced stumps. Average survival of unfenced stumps in 1989 was 59 percent, compared to 14 percent in 1997. In contrast, average survival of fenced stumps was 67 percent in 1989 and 54 percent eight years later. There were also significant differences between the survival of basal-cut stumps and those cut at 90 cm, with the taller stumps having twice the average survival of those cut at ground level (46 percent vs. 23 percent) *(table 2)*. This was consistent with results eight years earlier.

Table 2—*Survival (pct) of different treatments 10 years after harvest.*[1]

Fencing	Pct survival	Stump ht.	Pct survival	County	Pct survival	Season of harvest	Pct survival
Fenced	54 a	Basal	23 a	Mendocino	29 a	Summer	38 a
Unfenced	14 b	90 cm	46 b	Glenn	28 a	Fall	35 a
				Butte	44 a	Winter	36 a
				Amador	32 a	Spring	27 b
				San Luis Obispo	38 a		

[1] Values within a column are significantly different ($P<0.05$) if they are followed by a different letter (Fisher's protected LSD test).

Sprouting differences among sites were considerably less during the more recent assessment than they were in 1989 *(fig. 1)*, and there were no significant differences among them. Interestingly, while there were no significant differences in survival among harvest dates in 1988 and 1989, there were significant differences ($P=0.049$) in 1997, with the spring harvest date having significantly lower survival than the other three seasons of harvest *(table 2)*.

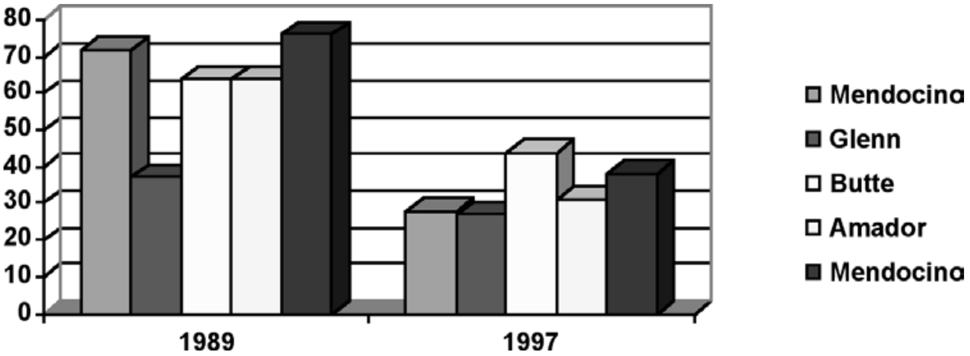

Figure 1—Percentage of stumps with living sprouts two and ten years after harvest (averaged over stump heights, harvest dates and protection treatments) at each harvest site.

Number of Sprouts

There were significantly more sprouts on stumps in unfenced plots than in fenced plots, and taller stumps had significantly more sprouts. There were also significantly more sprouts on stumps at the Mendocino site than at any of the other sites *(table 3)*.

Table 3—*Average number of sprouts from different treatments 10 years after harvest.*[1]

Fencing	No. of sprouts	Stump ht.	No. of sprouts	County	No. of sprouts
Fenced	6.1 a	Basal	7.2 a	Mendocino	18.2 a
Unfenced	10.7 b	90 cm	9.6 b	Glenn	6.5 b
				Butte	5.8 b
				Amador	6.2 b
				San Luis Obispo	6.1 b

[1] Values within a column are significantly different ($P<0.05$) if they are followed by a different letter (Fisher's protected LSD test).

Sprout Length

The lengths of the longest sprouts were significantly greater in fenced than unfenced plots; lengths were also greater for taller stumps *(table 4)*. There were significant differences in sprout length among harvest sites, with those in Mendocino and San Luis Obispo Counties having significantly shorter sprouts than those in Amador and Butte Counties.

Table 4—*Length of longest sprout (cm) from different treatments 10 years after harvest.*[1]

Fencing	Sprout length	Stump ht.	Sprout length	County	Sprout length
Fenced	246 a	Basal	131 a	Mendocino	101 a
Unfenced	113 b	90 cm	228 b	Glenn	177 ab
				Butte	259 b
				Amador	226 b
				San Luis Obispo	134 b

[1] Values within a column are significantly different ($P<0.05$) if they are followed by a different letter (Fisher's protected LSD test).

Sprout Diameter

Sprout diameter followed a pattern very similar to that for sprout length. There were significantly larger diameter sprouts for taller stumps and for stumps within fences *(table 5)*. Sprouts in plots in Amador and Butte Counties were significantly larger than those in Mendocino and San Luis Obispo Counties.

Table 5—*Diameter of largest sprout (cm) 10 years after harvest.*[1]

Fencing	Sprout diameter	Stump ht.	Sprout diameter	County	Sprout diameter
Fenced	4.2 a	Basal	2.6 a	Mendocino	1.6 a
Unfenced	2.0 b	90 cm	3.6 b	Glenn	3.2 b
				Butte	4.9 c
				Amador	3.9 bc
				San Luis Obispo	1.9 a

[1] Values within a column are significantly different ($P<0.05$) if they are followed by a different letter (Fisher's protected LSD test).

Decay

The decay of stumps did not vary by stump height or fencing, but there were some differences between sites, with Mendocino and Glenn having significantly greater average stump decay than the other three sites. Not surprisingly, decay ratings were significantly higher for stumps that did not have surviving sprouts than they were for stumps with living sprouts. Average values were 2.8 for the former, and 2.5 for the later.

Discussion

Sprouting is common for many species of hardwoods and it is likely that many of the oak trees that are alive in California today originated from sprouts that grew from a stump after the top was killed by fire or felling. Most sprout-origin trees are easily recognized because they often have multiple stems. In areas where fire destroyed the stand, or where all of the oaks were cut down at the same time, most of the trees have several stems and tree-ring studies reveal that many originated simultaneously (McClaran and Bartolome 1989, Mensing 1992), presumably from sprouting.

The ability of oaks to sprout from their base following death of the aboveground portion of the tree varies by species (Longhurst 1956), size of the individual tree (Johnson 1977), and environmental conditions at the site (Hannah 1987). Generally, sprouting is greater for evergreen or live oaks than for deciduous oaks; for smaller diameter stumps; and for trees growing in moister environments with more light. While blue oak is commonly thought of as a weak sprouter compared to tanoak and California black oak (McDonald 1990), the original assessment of the 960 trees harvested in this study found that a relatively large proportion (63 percent) had living sprouts two years after harvest (McCreary and others 1991). More smaller stumps sprouted than large ones, but we detected no differences in sprouting among the four seasons of harvest, in contrast to Longhurst (1956) who reported higher sprouting for blue oaks harvested in winter. Standiford and others (1996) also reported relatively high sprouting for blue oak in the northern Sacramento Valley, with 54 percent of the trees having sprouted, even though many stumps had originally been treated with herbicides to prevent re-growth.

As indicated above, one of the initial goals of this study was to try to identify variables that influenced sprouting so that harvesting in densely stocked stands could be used as a management tool to alter age structure. By promoting a more uneven age structure through harvest, it was hoped that stand longevity would be promoted and, even if natural regeneration was insufficient to replace mortality under natural circumstances, lengthening the life of stands might promote seedling recruitment since there would be a greater interval for this to occur. It was further speculated that opening the stands through thinning, and fencing out grazing and browsing animals, might also promote natural regeneration, though these effects were not evaluated in the study.

The data from this study suggests that sprouting can be used to alter age structure in stands, since even after 10 years, a sizeable number of the harvested trees have living, vigorous sprouts. However, it is also clear that sprouting is influenced by a number of variables. The most dramatic effects were from fencing, since in most locations, a decade of exposure to browsing animals resulted in high sprout mortality and reduced sprout growth. This effect was particularly evident at the plot in Mendocino County where high populations of deer from a resident herd, and additional pressures from a flock of sheep, resulted in a high proportion of the sprouts being killed and greatly reduced sprout growth on stumps that weren't fenced. High levels of browsing damage at this one site also resulted in several significant interactions between fencing and site. While all sites exhibited greater stump survival, sprout length, and sprout diameter in fenced plots compared to unfenced ones, the magnitude of these differences was far greater at the Mendocino plot than anywhere else.

At the Mendocino site heavy browsing in unfenced plots caused the average number of sprouts per stump to be approximately three times more at that location than anywhere else. The repeated browsing resulted in dense, brush-like sprout clumps on the few stumps that had surviving sprouts. Clearly, if one wishes to promote sprouting after harvest in areas with heavy browsing pressures, it is critical to protect stumps from browsing for at least 10 years.

While there were differences in sprout growth among sites, it is not clear what site variables were likely responsible for this. The site with the highest average annual precipitation (Mendocino) had the smallest average sprout length and diameter. Perhaps growth was influenced by environmental conditions associated with different elevations, since the sites with greatest growth (Butte and Amador) were at the two lowest elevations.

An initial concern was that taller stumps might decay more rapidly, causing sprouts to die. After 10 years there is no evidence that this is occurring. There were no significant differences in decay ratings between basal-cut stumps and those cut at 90 cm, and for almost all variables measured, taller stumps continued to perform better.

Conclusions

Results from this study indicate that even after 10 years, over a third of harvested trees have viable sprouts. However, there was considerable attrition in the eight years since the last assessment. The majority of sprout death during this 8-year interval appeared to be caused by browsing damage because the increase in mortality outside fenced exclosures was approximately four times that inside. In areas where browsing pressures are intense, either from livestock or deer, it is critical to protect sprouts. Season of harvest had relatively little impact on sprouting, but there was considerable variation in survival of sprouts, as well as sprout growth, among harvest sites. Sprouts from stumps cut at 90 cm continued to perform better than those cut at ground level, and there was no indication that these stumps deteriorated rapidly or that their sprouts died. Overall this study indicates that thinning of densely stocked blue oak stands can alter stand structure and will probably promote the establishment of a new, younger, cohort of trees. In this manner, it may prolong the life of stands, even when there is poor natural regeneration.

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Ten Years of Oak Restoration in City of Walnut Creek Open Spaces[1]

Ralph Kraetsch[2]

Abstract

The Oak Habitat Restoration Project began in 1991 when several individuals recognized that the oak woodlands and savannas of Walnut Creek's nearly 2,800 acres of open spaces had little natural regeneration. This group gathered volunteers who harvested acorns, planted them, and then installed tree shelters and watered the resulting seedlings. The Project soon became a unit of the Walnut Creek Open Space Foundation, which now provides most of our equipment and materials. The Project usually has 18 activity dates each year, nearly all on Saturday mornings. We usually plant 250 to 300 sites per year. About 75 percent of the sites initially contain at least one seedling from the three acorns planted in each site. At the end of the first growing season about 60 percent remain. We estimate that in 4 to 5 years about one-third of sites have become strong saplings. We have used a number of planting and maintenance methods which, over the years, have provided us with a preferred set of procedures that others may find useful.

Starting the Project

In 1989, Dick Daniel noticed that there were few oak seedlings and saplings in the Walnut Creek Open Spaces. He planted about 100 sites in a small fenced area in the open space and found very good success. During 1990, I made the same observation of lack of oak regeneration, and in the spring of 1991 Dick and I, together with Walnut Creek's newly hired Open Space Superintendent, Dan Cather, recruited volunteers for the Oak Habitat Restoration Project. The Project began with about 50 volunteers who typically attend 4 to 8 of our 18 activities per year.

We are fortunate that the City of Walnut Creek encourages our work and trusts the Project's judgment in restoration activities. This has enabled us to work with different restoration methods over the years until we found the methods we believe are well adapted to our warm and moderately dry climate.

The City provides storage space for our equipment and materials. The Project is now an activity of the non-profit Walnut Creek Open Space Foundation which funds most of our necessary equipment and materials. Vehicle needs are provided by volunteers. Grants from the California Native Plant Society, Chevron, and California ReLeaf and the California Department of Forestry and Fire Protection were important to our success in several of our early years.

Walnut Creek is located 22 miles directly east of San Francisco. In 1974 and 1975, the City acquired about 1,800 acres in four open space parcels on its periphery.

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[1] An abbreviated version of this paper was presented at the Fifth Symposium on Oak Woodlands: Oaks in California's Changing Landscape, October 22-25, 2001, San Diego, California.

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The open space now totals over 2,700 acres. These hilly oak woodland, savanna and chaparral areas were intensely grazed for many years prior to 1975, and this continued until 1990 when about 425 acres in Shell Ridge were withdrawn from grazing. In 1997 about 375 acres of Lime Ridge were withdrawn. These are the areas in which we have done most of our planting *(figs. 1 and 2)*.

Figure 1—Easterly view of Shell Ridge Open Space. Mt. Diablo is in the distant center.

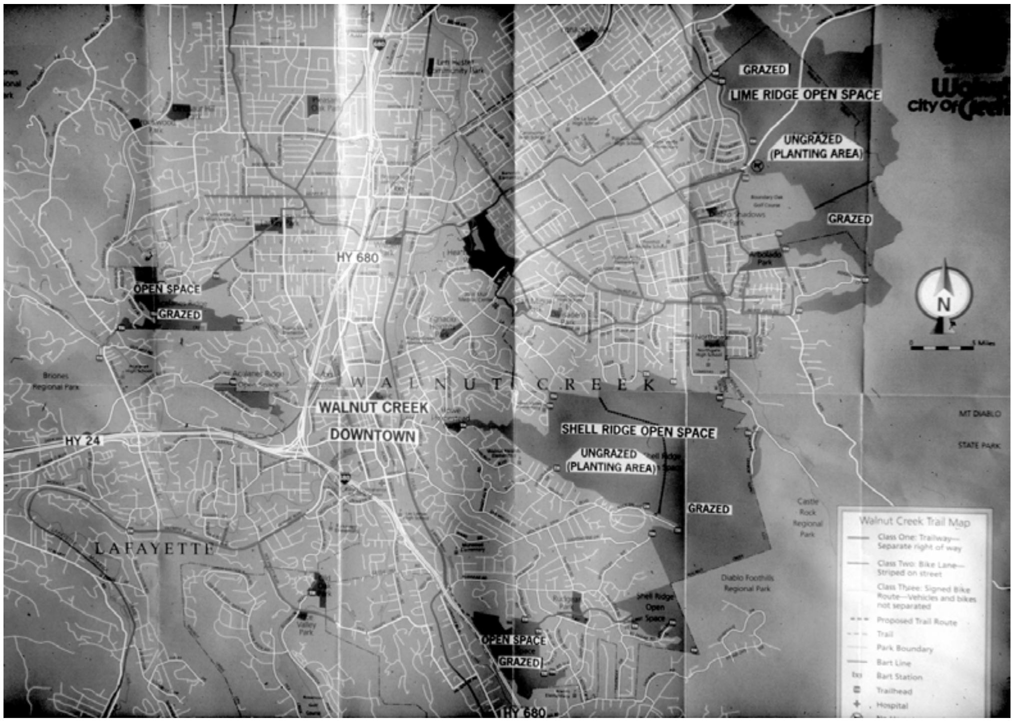


Figure 2—Location map of open spaces owned by the City of Walnut Creek showing ungrazed areas.

Procedures

Acorn Harvest

Our Project year begins in September with the acorn harvest. The crop varies widely from year to year and sometimes from species to species. We have three oak species, blue oak, valley oak and coast live oak *(Quercus douglasii, Q. lobata,* and *Q. agrifolia*) and we harvest only from open space trees to maintain local genetic integrity. In years with small acorn crops there is often a higher proportion of insect-damaged acorns so we tend to pick earlier, before maximum predation occurs. We continue picking as long as acorns hold on trees, usually after three harvest dates.

We provide volunteers with the following acorn harvest directions:

Equipment needed: 1 quart plastic collecting bags, swab pen for labeling bags, hook pole for harvesting acorns higher in tree (optional; use especially in years with poor acorn crop), larger bag for holding 1 quart bags.

1. Collect acorns only from a tree, never from the ground.
2. Remove caps and check acorns for damage before placing them in a collecting bag. Reject any acorn with damage to the base of the acorn, usually caused when removing the cap from an immature acorn. Also reject acorns with evidence of insects, bruises, cracks, misshapenness or very small. In years with poor acorn crops it may be necessary to keep some acorns with bruises or minor insect damage.
3. Use 1 quart collecting bags, no more than 100 acorns per bag, and be sure to label each with oak variety, date and general location.
4. Do not mix oak varieties in one bag. If you're not sure how to identify different varieties, ask!

We store acorns until planting in quart plastic bags, top partly open, in our refrigerator, just above freezing to retard sprouting and mildew. We dry the acorns monthly during storage to retard mildew, a somewhat laborious process.

We have found a significant difference in storage capability among our three oak species. Blue oak acorns sprout radicles and often develop mildew after just 3 to 5 weeks in storage. Valley oak acorns tend to sprout radicles 6 to 8 weeks after harvest, and are slower to develop mildew. Coast live oak acorns rarely develop radicles before 8 weeks, and many do not sprout for several months after harvest. Some of our 1999 coast live oak acorns stored in our refrigerator in partly open plastic bags within a closed heavy carton sprouted successfully when planted in mid-summer of 2000. Similarly, many coast live oak acorns collected in 2000 were viable in July 2001.

Planting

We begin planting after fall rains have moistened the soil to 8 to 10 inches and usually have five planting dates between late November and mid-January. We provide teams of two volunteers with the following directions for planting 10 sites.

Materials needed: 10 mulch mats, 40 mulch mat staples, 10 aluminum tags, 10 36-inch survey flags, ball point pen, trowel, clipboard with pre-numbered data sheet and procedures sheet, bag with 30 acorns, floral shovel. Units of 10 screen cylinders have been previously placed in the field *(fig. 3)*.

Figure 3—Equipment used for acorn planting.

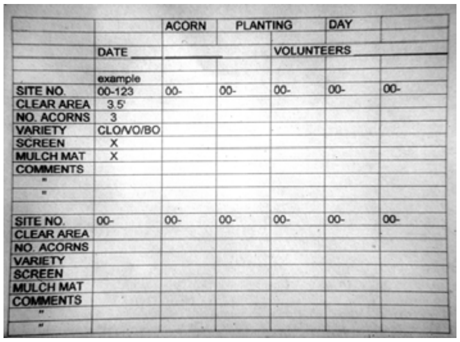
Procedures:

1. Select a site at least 50 feet from other plantings. Site should be on a sufficient slope that there will not be standing water during heavy rain periods.
2. With the shovel or other tool remove grass and weeds from an area 3+ feet square.
3. Dig a hole in the center of the cleared area about 8 inches deep. Keep the dirt within the cleared area for refilling the hole *(fig. 4)*.

Figure 4—Midway in planting site preparation.

4. Place a screen cylinder in the hole, at least 6 inches deep and fill inside the screen to about 1 inch below the surface level. Fill outside the screen to surface level. Tamp the filling to reduce future compaction, a major cause of failure due to acorn rot from water accumulation in a compaction "lake."

5. Place three acorns inside the screen, on their side, near the screen, points toward the center. Make a hole for any root (radicle) showing from the acorn. Fill inside the screen to ½ to 1 inch above the surface level.
6. Open the center slot of a plastic mulch mat about 1 inch on each side so the slot is just large enough to slip over the screen. Install the mat over the screen, shiny side up. Fold over the corners of the mat 3 to 4 inches and staple each corner through the folded layers of plastic.
7. With a ball point pen firmly write the site number on an aluminum tag (00-123, for example) using fairly large letters and attach the tag at the top of the screen. The “00” identifies the year of acorn harvest. The site number is preassigned on your data sheet.
8. Fill out the data sheet *(fig. 5)*.



		ACORN	PLANTING		DAY	
	DATE ____	____		VOLUNTEERS ____		
	example					
SITE NO.	00-123	00-	00-	00-	00-	00-
CLEAR AREA	3.5'					
NO. ACORNS	3					
VARIETY	CLO/VO/BO					
SCREEN	X					
MULCH MAT	X					
COMMENTS						
"						
"						
SITE NO.	00-	00-	00-	00-	00-	00-
CLEAR AREA						
NO. ACORNS						
VARIETY						
SCREEN						
MULCH MAT						
COMMENTS						
"						
"						

Figure 5—Acorn planting data sheet.

9. Pinch together the upper 1½ inches of the screen and fold this over about 45 degrees from vertical. DON'T FOLD TIGHTLY! We have to get back inside the screen in the spring to weed and install treeshelters.
10. Insert a survey flag through the three layers of screen. Don't bend the flag wire. Extend the flag as high as possible above the screen so we can locate the site after the grass grows tall in the spring *(fig. 6)*.

Figure 6—Completed planting site.

Spring Maintenance

Spring maintenance includes inspection of winter plantings, weeding inside screen cylinders and installing treeshelters on seedlings. Seedlings begin to emerge in mid-March. Some delay until early May, depending, we believe, on the planting date, acorn variety, depth of planting and amount of sun on the site. We weed all sites as we inspect them, whether or not a seedling can be found. Discovering new seedlings is a highly satisfying activity!

We provide teams of two volunteers with the following list of procedures for spring maintenance and treeshelter installation.

Materials: clipboard with data sheet and procedures list, pen, swab pen, trowel, 10 bird nets, small sledge hammer (10 Tubex treeshelters, 10 rebar posts and water are already in the field) *(fig. 7)*.

Figure 7—Equipment used for spring maintenance.

1. At a site, remove the flag, open the screen cylinder and look and feel for seedlings. You will often see mostly grass and weeds. Remove them. Oak seedlings are stiff and like a short brown blunt toothpick when they first emerge. Later a couple of small leaflets show.
2. If no seedling has yet emerged, or you're unsure whether something is actually a seedling, close the screen and replace the flag. We will recheck the site later in the spring.
3. If you find a seedling, after removing the grass and weeds, use a trowel to loosen the soil around the inside edge of the screen. If the soil is too firm, soften with some water. Of course, no damage to the oak seedling! Rotate the treeshelter into the soil at least 2 inches.
4. Push a rebar post through the plastic ties on the treeshelter and into the ground (use a hammer if necessary) below the top of the treeshelter if possible. Tighten the plastic ties. Add some water to settle the soil. Put a bird net over the treeshelter. Bend the top of the screen cylinder as necessary to minimize the space between the cylinder and the treeshelter to exclude rodents and lizards.

5. Complete the data sheet with the site number and seedling information. Dittos or arrows are fine for other notes.
6. Use the swab pen to place a 6+inch number reflecting the year of acorn harvest on the treeshelter visible from the nearest service road direction. This helps us identify which seedlings need to be watered during the summer.

The bird net is used to exclude birds who often perch on the treeshelter and occasionally fall in, killing themselves and usually any seedling present. The screen cylinder is left in place to protect the tender root system from rodent predation.

The Tubex treeshelters serve several purposes. Most important, they conserve moisture by recirculating daily condensation inside the shelter back down to the seedlings. The shelter also focuses summer watering on the seedling root system for deeper watering rather than spreading widely with shallow soil penetration. A third very important function of the treeshelter is discouraging predation by wildlife. We have found two sources of deer predation, browsing and antler rubbing on saplings in the fall.

We leave treeshelters on the plantings as long as the shelters hold together, many nearly 10 years at this time. Treessentials of Mendota Heights, MN (800-248-8239) is our supplier for the Tubex treeshelters, the plastic mulch mats and staples, as well as the small bags of slow release fertilizer we sometimes use in plantings.[3]

Summer Watering

We try to water seedlings for two summers to provide moisture during the critical summer dry period in their early years. We have no field source of water for piped irrigation, so we must carry water to the seedlings. Prior to the announced watering day we fill 1 and 1½ gallon plastic jugs and truck them to the planting area where they are dropped along service roads near the seedling sites. Volunteers then carry the water jugs to the seedlings, placing about ½ gallon in each treeshelter.

During the first watering sessions we inspect the plantings that have not yet shown a seedling. If a seedling does not show by June we recover the screen cylinder for reconditioning and reuse. At the end of the watering season we're already in the next acorn harvest.

Learning Experiences

Our learning experiences from these 10 years of restoration work are categorized into treeshelters and posts, screen cylinders, grazed area planting, fire effects and volunteer programs.

Treeshelters and Posts

We have experimented with various materials for the treeshelters, but have always returned to the stiff preformed plastic treeshelter under the Tubex brand. One

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[3] Mention of trade names or products is for information only and does not imply endorsement by the U.S. Department of Agriculture.

year we used a corrugated plastic material that is shipped flat and shaped into a treeshelter in the field. In parts of the country with cold winters this system is reported to have advantages. In our area these treeshelters begin to deteriorate within 2 to 3 years and form a fragmented mess that is difficult to clean up. We have also experimented with shelters made of heavy film. These are short, require wire exclosures and also deteriorated within 2 years.

In our early years we tried all available lengths of Tubex treeshelters, from 1 to 6 foot lengths. We no longer use the 5- and 6-foot shelters. Their original purpose was to protect seedlings from cattle browsing. We have found that seedlings have difficulty overtopping the taller shelters in our lower rainfall environment. The 1, 2 and 3-foot treeshelters require that we install exclosures to protect against deer browsing. Thus, the 4-foot treeshelters best satisfy our local needs.

In our first years we used T-bar fence posts to stabilize treeshelters. In order to reduce costs we then tried oak and redwood posts. The best of them rotted within 4 years. We have settled on ⅜-inch diameter rebar posts and find them cheaper than wood. In addition they can be recycled indefinitely.

Screen Cylinders

We tried a number of materials to build screen cylinders to defend the acorns from rodent and insect predation before settling on 24-gauge hardware cloth (screen). We purchase this material in 100-foot rolls of 2 foot width, cut it into 20 inch lengths and wire the resulting pieces into the 2 foot by 6 inch diameter cylinders. Lighter weight materials were too easily penetrated by our abundant ground squirrels.

Planting In Grazed Areas

We currently plant only in areas which are not grazed. In our early years we tried planting in grazed areas with disappointing results. The cost in materials and volunteer time is about double the cost for planting in ungrazed areas. Our method was to install a planting site as described earlier and add a 3½-foot diameter exclosure of 5 foot welded wire fencing stabilized with 2 or 3 rebar posts of ½-inch diameter. This is usually satisfactory where there are plenty of trees for cattle rubbing, but in areas with fewer trees our plantings became the principal rubbing target and were often severely damaged.

Fire Effects

Our single experience with fire 3 years ago showed it quite damaging to our plantings, but the effect can be short term. Heat melted the plastic treeshelters against the young oaks and killed the stems. However, we found that four of five plantings resprouted and grew rapidly from the undamaged root system.

Volunteer Programs

Volunteer recruitment has been a challenge over the years. The best sources have been members of our sponsoring Walnut Creek Open Space Foundation, the local Volunteer Center, open space kiosk signs and publicity in the local newspaper.

Occasional "Volunteer Day" programs sponsored by the City of Walnut Creek have been helpful, and one was the largest source for our beginning volunteer group.

Volunteer retention is also a problem. We have a core group of 12 to 15 who have been frequent participants over the years. Others come once or twice per year and still others find the activities too strenuous or not as interesting as they anticipated. A few others, largely the younger group, find new parenting or changed work responsibilities become higher priorities. Or they move out of the area. Teenage participants are welcome, but only a few attend more than once, usually to satisfy a high school community service requirement. The best volunteers are the newly retired who have not yet fully committed their time.

We publish a simple monthly newsletter, *Oak News,* which announces coming Project activities, notes volunteers present at recent field efforts, and comments on oaks, other native plants and general open space programs. We find the newsletter useful as an activity reminder, as an educational tool and to publicize the program to City officials and others.

Future Programs

In our early years we prepared for planting by dropping bundles of 10 screen cylinders at the 3 entrances to the Shell Ridge Open Space planting area. We found that areas distant from open space entrances received much less attention from volunteer planters than areas closer to the entrances. In recent years we have dropped the screen cylinders in the field at a number of locations closer to the target planting areas with much improved planting distribution.

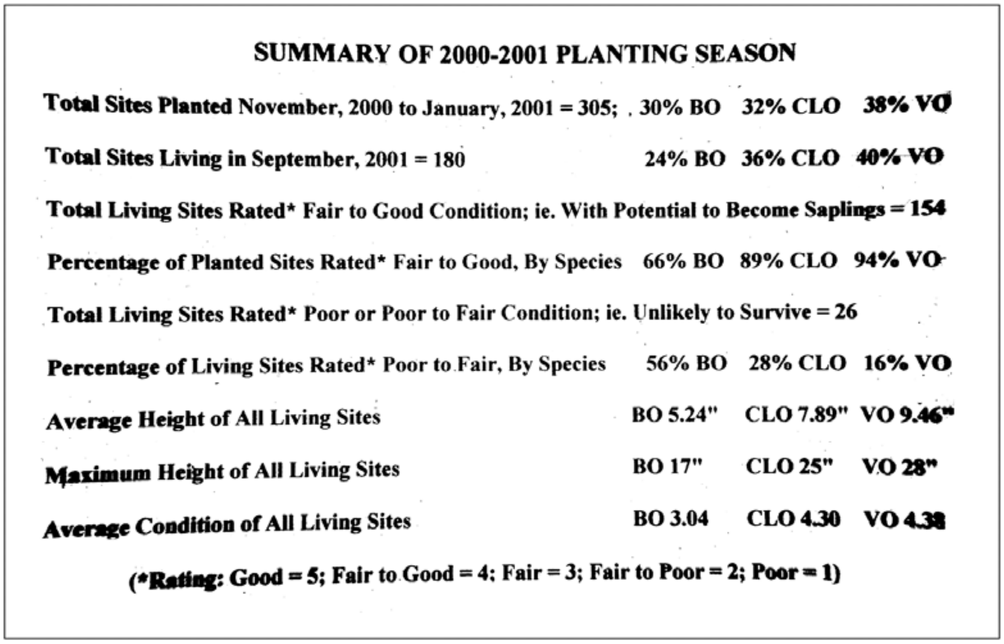
We are planning to try planting without screen cylinders in areas that are more difficult to reach so that volunteers will not need to carry full kits of materials long distances. This will involve planting about 20 acorns around a marker we can identify later. Then, after the grass dries we will return to these locations and search out any seedlings for installing treeshelters. Experiments with this method in past years haven't been successful. We will need to be especially careful to plant in areas without ground squirrels.

As noted earlier we have done most of our planting in the ungrazed areas of the City's open space. Many plantings in grazed areas have largely been severely damaged by cattle. In the future we hope to fence small plots, perhaps 20 to 30 foot squares, and plant several sites within each plot.

Results

We have recently made field checks of all surviving planting sites in order to compare our actual success with our estimates of success. Data from our first 6 years of planting in Shell Ridge Open Space is in poor condition so detailed analysis is not possible. We found 547 living sites from those plantings. Assuming an average of 300 sites planted per year yields a 30 percent success rate.

Analysis of sites planted during November 2000 to January 2001 with acorns harvested the previous September has provided much more useful results that will help direct our future planting methods and data recording *(fig. 8)*.



SUMMARY OF 2000-2001 PLANTING SEASON

Total Sites Planted November, 2000 to January, 2001 = 305; 30% BO 32% CLO **38% VO**

Total Sites Living in September, 2001 = 180 24% BO 36% CLO **40% VO**

Total Living Sites Rated* Fair to Good Condition; ie. With Potential to Become Saplings = 154

Percentage of Planted Sites Rated* Fair to Good, By Species 66% BO 89% CLO **94% VO**

Total Living Sites Rated* Poor or Poor to Fair Condition; ie. Unlikely to Survive = 26

Percentage of Living Sites Rated* Poor to Fair, By Species 56% BO 28% CLO **16% VO**

Average Height of All Living Sites BO 5.24" CLO 7.89" VO 9.46"

Maximum Height of All Living Sites BO 17" CLO 25" VO 28"

Average Condition of All Living Sites BO 3.04 CLO 4.30 VO 4.38

(*Rating: Good = 5; Fair to Good = 4; Fair = 3; Fair to Poor = 2; Poor = 1)

Figure 8—Status of November 2000 to January 2001 acorn planting season as of September 2001.

Conclusions

The preceding data analysis suggests several additions to our data recording. Topographic aspect of the planting site, soil character and possibly treeshelter diameter may help explain why some plantings are more successful than others. We can conclude that blue oaks, despite their abundance as living trees, have more trouble regenerating. We should plant four rather than three acorns in each blue oak site, and plant them early in the season, before mildew attacks elongated radicles. Analysis by planting date and correlation with rain periods may help increase efficiency of planting.

Our trial and error approach through this decade has led us to conclude that most of our current procedures are effective for a regeneration program of our size and budget in our environment. We welcome suggestions that may improve our results, and we will be happy to discuss our methods in more detail and provide field visits for those interested in our oak regeneration activities.

Modeling the Effectiveness of Tree Planting to Mitigate Habitat Loss in Blue Oak Woodlands[1]

Richard B. Standiford,[2] Douglas McCreary,[3] and William Frost[4]

Abstract

Many local conservation policies have attempted to mitigate the loss of oak woodland habitat resulting from conversion to urban or intensive agricultural land uses through tree planting. This paper models the development of blue oak (*Quercus douglasii*) stand structure attributes over 50 years after planting. The model uses a single tree, distance independent growth model, calibrated to data derived from a blue oak plantation. The results vary based on initial planting density and plantation management intensity. Data on crown cover, basal area, and average tree diameter and height are presented. For the range of modeled conditions, canopy cover after 50 years is projected to range from 7 to 33 percent, with an average DBH after 50 years ranging from 3.4 to 4.1 inches (8.6 to 10.4 cm). The cost of these tree replacement strategies is evaluated, and the effectiveness of tree planting as a mitigation tool, especially as it relates to the creation of wildlife habitat, is discussed.

Introduction

California has one of the most rapidly growing human populations in the world. The state's population has grown from less than 100,000 people in 1850, to over 31 million people today (an average annual rate of growth of 3.4 percent) to a projected 63 million people in the next 50 years (Medvitz and Sokolow 1995). This population growth is having an impact on oak woodlands. Although California's oak woodlands cover 7.4 percent of the state (Bolsinger 1988), and are the most biologically diverse broad habitat in the state (Pavlik and others 1991), they are also one of the most rapidly urbanizing areas in California (Duane 1999). A survey of oak woodland owners showed that the majority of all owners now live less than 5 miles (8 km) from a subdivision (Huntsinger and Fortmann 1990, Huntsinger and others 1997). This also showed that approximately one-third of the properties changed owners between 1985 and 1992, and 5 percent were subdivided for residential development.

Over the past 40 years, California's oak woodlands have decreased by over one million acres (405,000 ha) on a statewide scale (Bolsinger 1988) due to human-induced factors. Major losses from 1945 through 1973 were from rangeland clearing for forage production enhancement. Major losses since 1973 were from conversions to residential and industrial developments. Regionally, some oak woodlands have

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decreased from urban expansion (Doak 1989), firewood harvesting (Standiford and others 1996), range improvement (Bolsinger 1988), and conversion to intensive agriculture (Brooks and others 1999). Habitat fragmentation, increased conflicts between people with different value systems, predator problems, and soil and water erosion, have resulted. Blue oak woodlands (*Quercus douglasii* Hook. and Arn.), covering 23 percent of the state's woodlands (Bolsinger 1988), are one of the areas with the largest concerns about conversion.

Concerns about conserving the environmental values of oak woodland resources in the face of conversions to other land uses from rapid urbanization and changing agricultural markets, has led planners to develop strategies to mitigate these effects. Tree planting technologies for blue oak have improved tremendously in the past 15 years, and widespread success from planting is possible (McCreary 1990, McCreary 1995b, McCreary and Lippit 1996, McCreary and Tecklin 1993). Tree planting is often proposed as part of mitigation strategies to replace habitat losses (Giusti and Tinnin 1993, Bernhardt and Swiecki 1991, Fulton 1999). Many mitigation plans regularly call for tree planting on a replacement basis (1:1 to as high as 20:1) for trees lost. However, since there is little experience with growth rates of planted native oaks beyond 10 to 15 years, there has not been an opportunity to assess how oak woodland habitats will develop over time from areas planted, and whether this mitigation approach on overall habitat quality is effective.

The purpose of this study was to evaluate blue oak tree planting as a mitigation strategy for habitat loss. The results should help assess the long-term impacts of tree planting on oak woodland habitat development.

There have been a number of studies evaluating growth of blue oak seedlings, and reporting on height, diameter, and canopy development with various management strategies (McCreary 1990, 1995a, 1995b; McCreary and Lippit 1996; McCreary and Tecklin 1993). There is no information on stand structure development extending beyond 10 to 15 years. There have been several long term whole stand growth models of blue oak woodlands developed by Pillsbury and DeLasaux (1985), and Standiford and Howitt (1988, 1993). However, these do not provide detailed information on stand structure development, but only general volume and basal area growth. A single tree, distance independent growth model has been developed for blue oak natural stands (Standiford 1997) which offers some promise for a more detailed assessment of stand development.

Methods

This study utilized a modeling approach to evaluate blue oak plantation development. *Figure 1* depicts the model used to predict the attributes of a planted stand over time. The individual tree size data (height, diameter, crown spread) 10 years after planting provided the input variables for the model. Individual tree basal area growth was modeled as a function of tree size, competition of each tree with adjacent trees, and site quality (Standiford 1997). Individual tree height growth and canopy development were correlated with basal area increment. The summation of the individual trees provided the stand totals for the first 10 years (basal area per acre, average DBH, average height, crown cover percent). The tree list and stand attributes were updated for every 10-year interval by a growth model that was based on actual blue oak stand age and structure data (Standiford 1997). Woodland productivity was assessed with a height-diameter site index relationship developed for blue oak sites

(Standiford and Howitt 1988). This was derived to give an index number for the height of a dominant tree in a stand when it averages 10 inches (25 cm) diameter at breast height (DBH). A site index of 50 feet (15 m) was assumed for the models presented below, which means that when the dominant trees average 10 inches (25 cm) DBH, they will average 50 feet (15 m) in height.

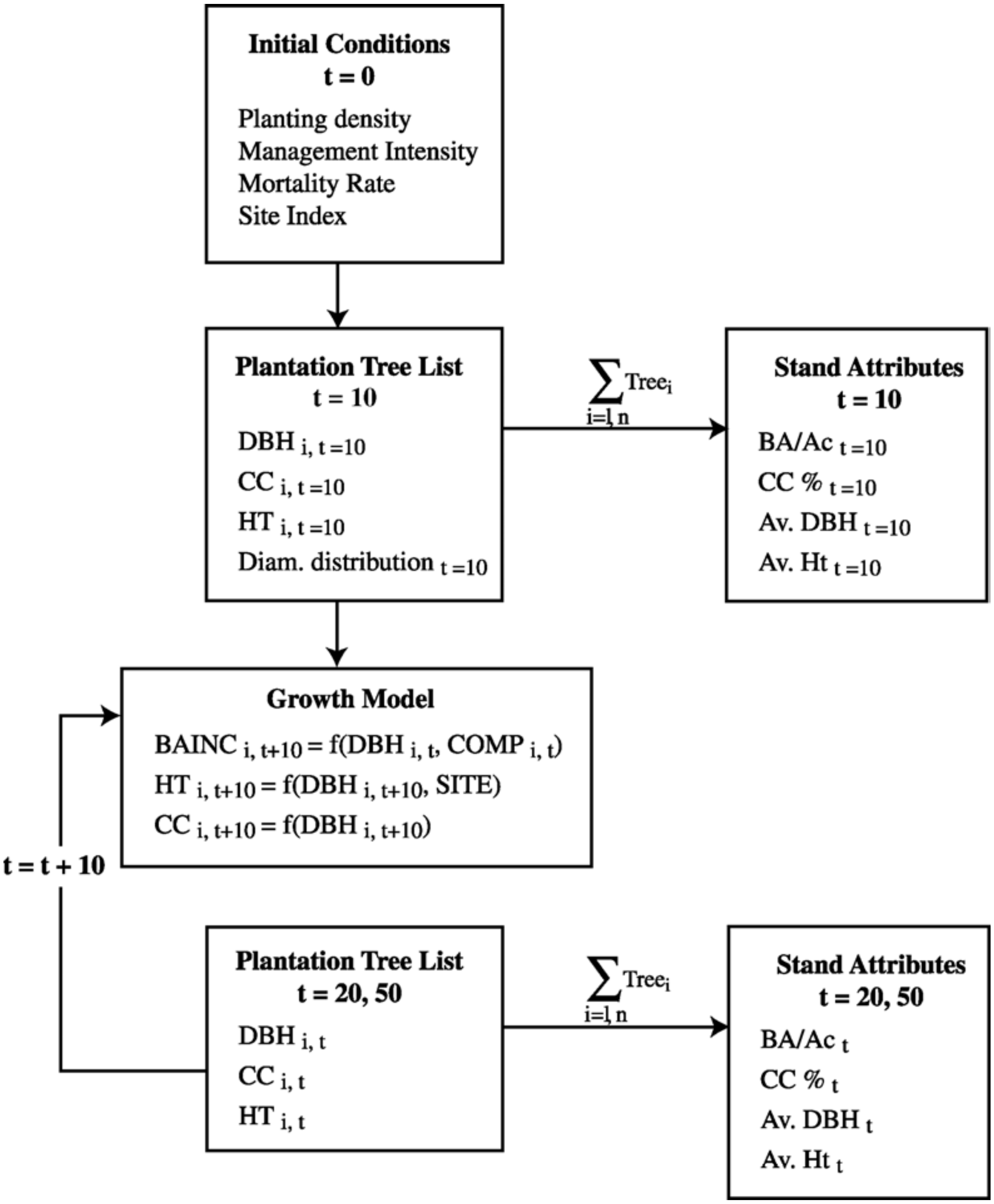

Figure 1—Modeling schematic to evaluate individual tree growth and stand characteristics of planted blue oaks over time. Where: DBH $_{i,t}$ is diameter at breast ht. (4.5 ft) of tree i at time t, CC $_{i,t}$ is canopy cover in sq. ft. of tree i at time t, HT $_{i,t}$ = total height of tree i at time t; BAINC $_{i,t+10}$ is basal area increment model for tree i for ten year period after time t, COMP $_{i,t}$ = competition index (Standiford 1997) for tree i at time t, BA/Ac $_{t}$ = stand basal area in square feet per acre at time t.

Data was collected from 55 sample blue oak trees in a ten-year old blue oak plantation at the Sierra Foothill Research and Extension Center (SFREC) in Yuba County, California, approximately 40 miles (64 km) northeast of Sacramento. The correlation between individual tree basal area and height and crown surface area was evaluated.

Based on the yield table of modeled stand attributes, a general assessment of wildlife habitat relationships was made using the Version 7.0 California Wildlife Habitat Relationships (CWHR) model (Giles and others 1999). The modeled stand is referred to as a "mitigated stand" since it represents tree planting designed to mitigate expected environmental impacts from tree removal in a particular project. The CWHR habitat types were evaluated based on the attributes of the mitigated stand, and applying the classification rules for CWHR (Mayer and Laudenslayer 1988). The list of vertebrate species generated by CWHR for the mitigated stand at different time periods was compared to a natural mature blue oak stand. These differences in vertebrate species were evaluated to see how the mitigated stand compared to the habitat lost in the mature stand.

Results

A regression equation was developed to predict the height and crown canopy area of the individual trees on the basis of the basal area of the individual tree at breast height (derived from DBH). This relationship helped to assess height and crown changes of the planted trees over time, for which there were no existing growth models. Equations 1 and 2 show the results of the regression of blue oak plantation tree height and crown surface area with individual tree basal area. A logarithmic form was utilized to represent the curvilinear shape of the relationship.

$$\ln(HT_i) = \underset{(**)}{3.164} + \underset{(**)}{0.213} \times \ln(BA_i) \qquad R2 = .67 \tag{1}$$

$$\ln(CC_i) = \underset{(**)}{5.018} + \underset{(**)}{0.427} \times \ln(BA_i) \qquad R2 = .60 \tag{2}$$

where: CC_i is canopy cover of tree i in square feet per tree, HT_i is total height of tree i in feet, BA_i is basal area of tree i at breast height (4.5 feet) in square feet per tree, ln is natural logarithm, and ** is significant at 0.01 level

These equations were applied to individual tree basal area, and basal area after growth projections, to develop tree height and crown cover for each tree. The initial tree list was based on diameter distribution data for a plantation that was monitored for 10 years after planting. Two different management regimes were assumed. A high management intensity scenario assumed that complete weed control was maintained for a 3-year period, and that best management strategies for planting seedlings were followed (McCreary 1995a). The assumption is that these stands would average 2 inches (5 cm) DBH after 10 years, and there would be a 90 percent seedling survival. The moderate management scenario assumed that weed control was for the first year only, resulting in stands averaging 1.5 inches (3.8 cm) DBH, with an 85 percent seedling survival. These assumptions are based on actual plantation growth

(McCreary 1990, 1995a, 1995b; McCreary and Lippit 1996; McCreary and Tecklin 1993) and observations of operational restoration projects.

Table 1 shows the results of the simulation of the blue oak mitigation planting. Initial planting densities were evaluated from 100 to 400 trees per acre (247 to 988 trees per hectare) for both the high and moderate management intensities. These results show that for both the high and moderate intensity category, planting only 100 trees per acre (247 trees per hectare) does not result in a stand with over 10 percent canopy cover after 50 years. Mature blue oak stands may only have 40 to 50 trees per acre (99 to 124 trees per hectare) (Bolsinger 1988), so planting 100 trees per acre (247 trees per hectare) would represent a 2:1 replacement strategy. After 50 years, these planted stands would still be classed as annual grasslands by the CWHR classification system since tree canopy cover is less than 10 percent.

Table 1 also shows the CWHR habitat seral stages for the mitigated stand over the 50-year simulation period. The two habitat stages projected to occur in the planted stands 50 years from establishment (Blue oak 2S and Blue oak 2P) were evaluated with the CWHR model. Since the purpose of the modeling was to evaluate the impacts on wildlife species associated with the hardwood tree component of blue oak woodlands, the list of species was reduced by eliminating species primarily associated with aquatic or conifer habitats, and species with an average habitat quality less than "medium." The area chosen for study was the central Sierra Nevada foothills. The results of the vertebrate wildlife projected to occur in these stands showed that 73 species would have medium or high quality habitat values in the two habitat stages projected to exist in planted stands in 50 years (1 amphibian, 40 bird, 19 mammal, and 13 reptile species).

The mitigated stand species list was compared to a natural blue oak stand, averaging 10 inches (25 cm) DBH, with a 30 percent canopy cover (Blue Oak 3P seral stage). The natural stand is assumed to have small and medium size downed wood, snags, acorns and trees with cavities. A natural stand with this habitat condition is projected to have 102 vertebrate wildlife species with medium or good habitat. The impacts were compared by evaluating the percent change in habitat quality between the natural and mitigated stand, using equation 3 below:

$$\left(\frac{H_{nat} - H_{mit}}{H_{nat}}\right) \times 100 = \text{Percent change} \qquad (3)$$

where: H_{nat} is habitat quality for natural stand, H_{mit} is habitat quality for mitigated/planted stand.

Garrison (1994) points out the difficulties in determining the biological significance of CWHR predictions. Garrison and Standiford (1997) address the tenuous nature of these predictions by utilizing a 50 percent change as the significant impact threshold. This is considered a relatively conservative threshold, representing an average habitat suitability change of at least one rating class.

Table 1—*Modeled blue oak stand characteristics after planting*

Planting density	Management intensity[1]	Age yrs.	Crown cover pct.	Basal area sq. ft/ac (sq. m/ha)	Av. diam. breast ht. in. (cm)	Av. height ft. (m)	CWHR seral stage[2]
100 trees per acre (247 trees per hectare)	High	10	6	2.0 (0.5)	2.0 (5.1)	11 (3.4)	AG 1D
		20	7	3.0 (0.7)	2.6 (6.6)	14 (4.3)	AG 1D
		30	7	4.2 (1.0)	3.1 (7.9)	15 (4.6)	AG 1D
		40	8	5.4 (1.2)	3.6 (9.1)	18 (5.5)	AG 1M
		50	9	6.7 (1.5)	4.1 (10.4)	21 (6.4)	AG 1M
	Moderate	10	4	1.1 (0.3)	1.5 (3.8)	10 (3.0)	AG 1D
		20	5	1.9 (0.4)	2.1 (5.3)	12 (3.7)	AG 1D
		30	6	2.8 (0.6)	2.6 (6.6)	14 (4.3)	AG 1D
		40	7	3.8 (0.9)	3.1 (7.9)	15 (4.6)	AG 1D
		50	7	4.9 (1.1)	3.6 (9.1)	18 (5.5)	AG 1D
200 trees per acre (494 trees per hectare)	High	10	12	4.1 (0.9)	2.0 (5.1)	11 (3.4)	BO 2S
		20	13	6.0 (1.3)	2.5 (6.4)	14 (4.3)	BO 2S
		30	15	8.1 (1.9)	3.0 (7.6)	15 (4.6)	BO 2S
		40	16	10.4 (2.4)	3.5 (8.9)	18 (5.5)	BO 2S
		50	17	12.8 (2.9)	4.0 (10.2)	20 (6.1)	BO 2S
	Moderate	10	9	2.2 (0.5)	1.5 (3.8)	10 (3.0)	AG 1M
		20	11	3.6 (0.8)	2.0 (5.1)	12 (3.7)	BO 2S
		30	12	5.3 (1.2)	2.5 (6.4)	13 (4.0)	BO 2S
		40	13	7.3 (1.7)	3.0 (7.6)	15 (4.6)	BO 2S
		50	14	9.3 (2.1)	3.5 (8.9)	17 (5.2)	BO 2S
300 trees per acre (741 trees per hectare)	High	10	18	6.1 (1.4)	2.0 (5.1)	11 (3.4)	BO 2S
		20	20	8.9 (2.0)	2.5 (6.4)	14 (4.3)	BO 2S
		30	22	11.9 (2.7)	3.0 (7.6)	15 (4.6)	BO 2S
		40	24	15.3 (3.5)	3.5 (8.9)	17 (5.2)	BO 2S
		50	25	18.8 (4.3)	3.9 (9.9)	20 (6.1)	BO 2P
	Moderate	10	13	3.3 (0.8)	1.5 (3.8)	10 (3.0)	BO 2S
		20	16	5.4 (1.2)	2.0 (5.1)	12 (3.7)	BO 2S
		30	18	7.9 (1.8)	2.5 (6.4)	13 (4.0)	BO 2S
		40	20	10.6 (2.4)	3.0 (7.6)	14 (4.3)	BO 2S
		50	21	13.6 (3.1)	3.5 (8.9)	17 (5.2)	BO 2S
400 trees per acre (988 trees per hectare)	High	10	24	8.2 (1.9)	2.0 (5.1)	11 (3.4)	BO 2S
		20	27	11.8 (2.7)	2.5 (6.4)	14 (4.3)	BO 2P
		30	29	15.8 (3.1)	3.0 (7.6)	15 (4.6)	BO 2P
		40	31	20.1 (4.6)	3.4 (8.6)	17 (5.2)	BO 2P
		50	33	24.6 (5.1)	3.9 (9.9)	20 (6.1)	BO 2P
	Moderate	10	18	4.3 (1.0)	1.5 (3.8)	10 (3.0)	BO 2S
		20	21	7.1 (1.6)	2.0 (5.1)	12 (3.7)	BO 2S
		30	24	10.3 (2.4)	2.5 (6.4)	13 (4.0)	BO 2S
		40	26	13.9 (3.2)	3.0 (7.6)	14 (4.3)	BO 2P
		50	28	17.8 (4.1)	3.4 (8.6)	17 (5.2)	BO 2P

[1] Management Intensity Assumptions—10 years after Planting—High–average 2 inches (5 cm) DBH with 90 percent survival; Moderate–1.5 inches (3.8 cm) DBH with 85 percent survival.

[2] CWHR Seral Stages—AG 1D is annual grassland, grass height less than 12 inches (0.3 m), over 60 pct. cover; AG 1M is annual grassland, grass height less than 12 inches (0.3 m), 40 to 59 pct. cover; BO 2S is blue oak woodland, 1-6 in. (2.5 to 15.2 cm) DBH, 10-24 pct. cover; BO 2P is blue oak woodland, 1-6 in. (2.5 to 15.2 cm) DBH, 25-39 pct. cover.

The mature blue oak (3P) was compared to planted blue oak stands (2P and 2S). The mitigation resulted in 17 species that showed significant decreases in habitat compared to the natural stand. For the 2S seral stage (projected to occur with planting densities of 200 trees per acre), 18 species had a significant increase in habitat quality after the mitigation. There were 10 species with a significant increase in habitat quality for the 2P seral stage (projected to occur with planting of 300 to 400 trees per acre [740 to 988 trees per hectare]). Seventy-five species had no significant change in quality for the 2S stage, and 67 had no change for the 2P stage.

The species that were projected to have significant decreases in habitat suitability were acorn and cavity dependent species such as various woodpecker species, the western bluebird, and the western gray squirrel. Species with significant increases in habitat suitability were wildlife that prefer meadows and open stand types, including the California pocket mouse, the California vole, the horned lark, and the Western meadowlark.

Discussion

This approach provides planners, developers and the restoration community with a tool to evaluate how important characteristics of the stand will develop over time. The projected structure of planted blue oak stands over a 50 year period from this study can be compared directly to actual stand data for areas that will possibly be lost in a conversion project that will need mitigation.

The general results of this study raise questions as to whether the structure of planted stands adequately mitigate the loss of mature stands. As these results show, average tree size after 50 years under fairly aggressive restoration efforts, is still quite small. The largest mean diameter of the stand is only 3.9 inches (9.9 cm), with a canopy cover of 33 percent.

Using CWHR as a tool to evaluate the wildlife habitat quality of the planted stand showed that in general, the overall biodiversity figures are not greatly affected from the mature stand chosen for comparison in this paper. However, the species composition shifts from wildlife species that utilize cavities, acorns, and downed wood, to species that utilize open meadows and grasslands.

Another factor to be considered is the cost of tree planting as a mitigation strategy. Although planting technology has advanced tremendously, restoration costs may range from $210 (moderate intensity) to $280 (high intensity) per acre for 100 trees per acre ($519 to $692 per hectare for 247 trees per hectare), up to $470 (moderate intensity) to $765 (high intensity) per acre for 400 trees per acre ($1161 to $1890 per hectare for 988 trees per hectare) (Standiford and Appleton 1993). These costs were updated to 2001 dollars using the producer price index. In some cases, it may be more cost effective to utilize the mitigation funds to ensure that existing mature habitat is conserved, through the purchase of conservation easements, the set aside of large blocks of commonly-owned land and density credits, or the establishment of public open space.

Conclusion

The results suggest that it is important to evaluate if tree planting is a viable method of mitigation. It appears to be a very costly, long-term effort, to restore an area. Many important habitat elements, such as cavities, acorns, snags, and woody debris may not be mitigated - at least in the 50-year interval evaluated in this study - through a tree planting strategy alone. Although procedures for discounting habitat decreases for woodland species and habitat increases for meadow species are not established, the results can be used as part of discussions about appropriate mitigation strategies.

These results rely on modeling extrapolated from relatively young tree plantations and natural stand growing conditions. It will be important to consider if the long-term growth of planted stands follows these preliminary projections. Actual height and crown growth models are needed, rather than relying on the correlation with basal area growth. Continued evaluation of planted stands is required to develop these improved models. It is also important to conduct on-site wildlife evaluations to determine the reliability of CWHR projections.

Although the results of this work point out that blue oak plantations develop habitat conditions slowly, and it may take in excess of 50 years to replace mature habitat that is lost in a particular project, tree planting is still an important conservation tool. The great strides that have been made in oak planting on hardwood rangelands should still be encouraged as part of an overall restoration strategy. Effective mitigation, however, may well require a more diverse array of tools to address the impacts of various woodland conversion projects.

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Monitoring California's Hardwood Rangelands Using Remotely Sensed Data[1]

Chris S. Fischer[2] and Lisa M. Levien[3]

Abstract

As human and natural forces continue to alter the hardwood landscape, resource agencies, county planners and local interest groups find it increasingly important to monitor and assess these alterations. The California Land Cover Mapping and Monitoring Program (LCMMP), a cooperative program between the USDA Forest Service and the California Department of Forestry and Fire Protection, is addressing statewide long-term monitoring strategies using Landsat Thematic Mapper (TM) satellite imagery. The LCMMP creates seamless vegetation and monitoring data across California's landscape for regional assessment across all ownerships and vegetation types. This paper focuses on the hardwood rangeland region from Shasta County in the north to Kern County in the south, extending from 300 to 5,000 feet in elevation. Results indicate that most of the hardwoods did not undergo change between 1991 and 1996. However, large change did occur in concentrated areas from wildfire, harvest and development. Regeneration of hardwoods was also detected. The LCMMP directly addresses CDF's need for a long-term monitoring strategy to inform discussion of issues centered on California's hardwood rangelands. CDF now has the ability to identify trends in hardwood rangeland structure, health, resource use and other factors that affect long-term viability across large regions. The LCMMP provides critical information on the impacts management decisions and natural forces have on the environment. This information includes the actual location and extent of change, three levels of vegetation cover increase and decrease and the cause of change. Knowing the location and extent of vegetation change provides a picture of the distribution and concentration of change areas. Levels of change give an indication of vegetation removal, vigor or health. Understanding what is causing these changes creates an awareness of the impacts change agents have on the landscape. This information is useful to assess the effectiveness of existing policies, programs, management activities and regulations, and to develop alternatives as needed (e.g., county voluntary guidelines for oak woodland management).

Introduction

Hardwood rangelands are one of California's most expansive and biologically diverse ecosystems (Pavlik and others 1991). They cover just over 10 million acres and occur in 47 of 58 counties, with most in private ownership (Greenwood and others 1993). Characterized by an oak overstory and a grass, forb and brush understory, hardwood rangelands provide many ecological and commercial values,

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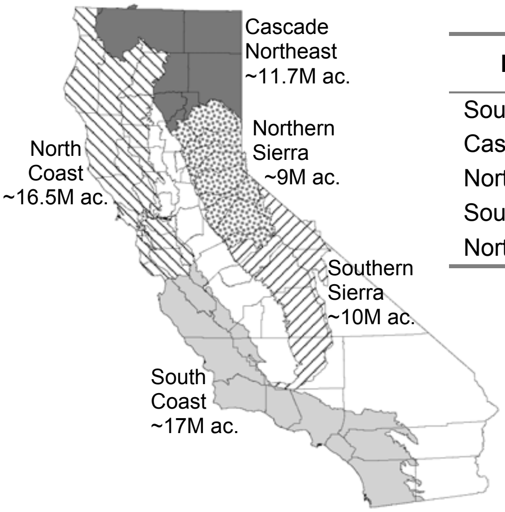
including wildlife habitat, water quality, erosion control, livestock grazing, vineyard production, recreation and urban centers.

Historically, California's hardwood rangelands have been under constant pressure from intensive agriculture, range production and fuelwood harvesting. Between 1945 and 1988, approximately 1.2 million acres of hardwood rangeland were lost due to agricultural conversion (Bolsinger 1988). More recently, threats are occurring from residential and commercial development and agricultural expansion. Many new developments are emerging in hardwood rangelands because they are predominantly in private ownership and near population centers (Scott and others 1995). Urban expansion has a profound effect on hardwood resources as development generally fragments the landscape. Agricultural conversion to high value crops, such as vineyards, is increasing particularly in coastal counties (Merenlender 2000). Studies also suggest that many oak species are not naturally regenerating adequately, further impacting this resource (Adams and others 1990, McCreary 1991).

As human and natural forces (e.g., mortality, wildfire) continue to alter the hardwood landscape, resource agencies, county planners and local interest groups find it increasingly important to monitor and assess these alterations. In 1987, the State Board of Forestry recognized this need and directed the California Department of Forestry and Fire Protection (CDF), the California Department of Fish and Game (CDFG), and University of California Cooperative Extension to develop the Integrated Hardwood Range Management Program (IHRMP), a non-regulatory program to resolve hardwood issues through research, education and monitoring (UC and CDF 1994). A long-term effort to address monitoring needs began with the development of a baseline map of California’s oak woodlands derived from 1981 aerial photography (Pillsbury and others 1991). Later, satellite imagery was used to create a more current map of hardwood rangelands and compare it to the earlier aerial photo base map (Pacific Meridian Resources 1994). Satellite data proved to be a useful tool to address monitoring over large areas, when coupled with adequate field verification (UC and CDF 1994).

In 1995, a cooperative program between the USDA Forest Service (USFS) and CDF was launched to address long-term monitoring strategies (Levien and others 1996). This program is formally called the California Land Cover Mapping and Monitoring Program (LCMMP). The objective of the LCMMP is to create seamless vegetation and monitoring data across California’s landscape for regional assessment across all ownerships and vegetation types. The program uses Landsat Thematic Mapper (TM) satellite imagery to derive land cover change over 5-year time periods *(fig. 1)*. These monitoring data provide critical information on the impacts of vegetation change over large areas. They also provide timely data for the CDF and IHRMP to assess statewide trends in hardwood rangeland ecosystems, and for planners, resource managers, landowners, industry, watershed groups and others for land use planning, biological diversity assessment, resource management and sustainable economic development.



Project area	Monitoring dates (nominal)	Change data complete
Southern Sierra	1990 to 1995	1996
Cascade Northeast	1991 to 1996	1997
Northern Sierra	1991 to 1996	1997
South Coast	1993 to 1997	1999
North Coast	1994 to 1998	2000

Figure 1—Location and extent of project areas with first statewide monitoring schedule.

Methods

This paper focuses on the hardwood rangeland region from Shasta County in the north to Kern County in the south, extending from 300 to 5,000 feet in elevation. A total of eight TM scene pairs cover the project area *(fig. 2)*. Scene path/row and dates are displayed in *table 1*. All images were co-registered using a third-order affine transformation model. The LCMMP detects changes in land cover between two different TM image dates. Images are selected during the late summer season of each year (e.g., August 1991 and 1996) to ensure that the processes of canopy maturation and senescence and the growth cycle of understory grasses do not interfere with actual land cover changes. Steps required to produce a final change image include database building, change processing, change labeling and accuracy assessment.

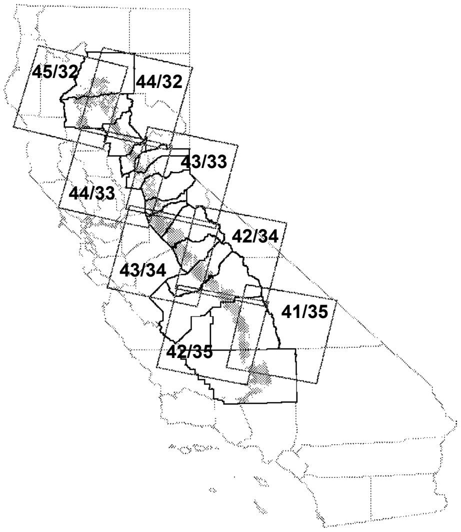


Figure 2—Location of project area and TM scenes. Grey area is hardwood rangeland.

Table 1—*TM imagery for project area.*

Path/row	Dates	
45/32	6/27/90	8/14/96
44/32	8/26/91	8/07/96
44/33	6/20/90	8/07/96
43/33	7/02/91	7/31/96
43/34	8/16/90	9/15/95
42/34	8/25/90	9/08/95
42/35	8/25/90	9/08/95
41/35	9/0390	9/17/95

Database Building

In this procedure, TM imagery is prepared for processing and a seamless vegetation layer is assembled. The first step in preparing the TM imagery is to register the early date TM image to the later date TM image that is in the same path and row. Registration begins by identifying common features throughout both images on-screen (e.g., road intersections). Approximately 50 to 100 features are located throughout each scene pair. These features are used in a nearest neighbor resampling technique to assign the early date pixel values to the later date pixel locations. Nearest neighbor resampling avoids altering pixel values, therefore maintaining spectral reflectance of ground features. These new pixel locations must be within a one-half pixel of the later date pixels to eliminate any false changes. The images are then radiometrically corrected to account for differences in atmospheric conditions (e.g., haze and water vapor). This correction is accomplished by extracting invariant light (rock outcrops) and dark (water bodies) features from both dates of imagery and running a regression-based correction on the resulting pixels (Schott and others 1988). The regression equation is applied to the early date TM image to derive normalized pixel values.

Land cover data are used to determine which vegetation types are experiencing change. The LCMMP produces vegetation data using the Classification and Assessment with Landsat of Visible Ecological Groupings (CALVEG) (USDA Forest Service Regional Ecology Group 1981) and Wildlife Habitat Relationships (WHR) (Mayer and Laudenslayer 1988) classification systems. However, geographic extent is not complete for the state; thus, other vegetation data sources are required to attain full project area coverage. Other data sources include a hardwood data layer (CDF layer updated in 1990) and a GAP data layer (created in 1990). Vegetation layers are mosaicked with precedence given to the LCMMP layers, then the updated hardwood layer and finally the GAP layer. GAP data is usually a small component of the seamless vegetation layer and mainly is used to cover the low elevation valley areas.

Change Processing

Co-registered and radiometrically corrected TM imagery is analyzed for change using image processing techniques. A Kauth-Thomas transformation is applied to a 12-band image (bands 1-5 and 7 from each date) (Kauth and Thomas 1976). This transformation applies coefficients to each TM band producing a new image depicting changes in brightness, greenness and wetness components *(table 2)* (Crist and Cicone 1984). These brightness, greenness and wetness components are calculated by the equation:

$$Bt1 = B1(TMb1)+B2(TMb2)+B3(TMb3)+B4(TMb4)+B5(TMb5)+B7(TMb7)$$

$$Gt1 = G1(TMb1)+G2(TMb2)+G3(TMb3)+G4(TMb4)+G5(TMb5)+G7(TMb7)$$

$$Wt1 = W1(TMb1)+W2(TMb2)+W3(TMb3)+W4(TMb4)+W5(TMb5)+W7(TMb7)$$

where Bt1 is the brightness value for time 1; Gt1 is the greenness value for time 1; Wt1 is the wetness value for time 1; Bx is the brightness coefficient for TM band x; Gx is the greenness coefficient for TM band x; Wx is the wetness coefficient for TM band x; and TMbx is the TM band x reflectance value. Brightness is a measure of overall reflectance, greenness is related to the amount of green vegetation present in the scene, and wetness correlates to canopy and soil moisture (Crist and others 1986). The change in BGW differentiates change in vegetation cover over the time period. In order to reduce the amount of information from the resulting BGW change image, we aggregate pixels into polygons using a segmentation algorithm. This algorithm is a multipass algorithm that uses several parameters to define the threshold of similarity between neighboring pixels (Ryherd and Woodcock 1990).

Table 2—*Kauth-Thomas coefficients for TM imagery.*

	TM1	TM2	TM3	TM4	TM5	TM7
Brightness	0.2147	0.1975	0.3354	0.3949	0.3593	0.1317
Greenness	-0.2017	-0.1724	-0.3848	0.5116	0.0589	-0.1275
Wetness	0.1067	0.1395	0.2318	0.2408	-0.5029	-0.3233

Change Labeling

The resulting change image is then stratified by individual lifeform type (e.g., conifer, hardwood, shrub) using the composite vegetation layer. An unsupervised classification is applied to each change image by lifeform, which results in approximately 50 change classes per lifeform type change image. Within each of these, categories of similar levels of brightness, greenness and wetness values are assigned to one of nine change classes that include large decrease, moderate decrease, small decrease, large increase, moderate increase, small increase, non-vegetation change and little to no change. Image appearance, photo interpretation, vegetation and topographic maps and bispectral plots (e.g., greenness vs. wetness) aid in assigning the change classes. Each individual lifeform change image is then mosaicked into one project area change map.

Decrease and increase change classes represent relative changes in vegetation cover. For example, a small decrease will have less vegetation cover loss than a moderate or large decrease (e.g., a forest thinning compared to a clearcut). The little to no change class indicates that change did not occur or that change was so slight that it could not be detected. The non-vegetation change class accounts for variations in lake or reservoir water levels and snow pack in the higher elevations. A cloud and shadow class is added to account for clouds in the imagery and shadows in the mountainous areas that obscure ground cover making it impossible to determine whether the vegetation had changed or remained stable in these areas.

Accuracy Assessment

A total of 300 randomly selected change areas were compared with known reference information of the same areas. All change classes were represented with sites based on the acreage amount of change (e.g., the little to no change class has the largest acreage, thus contains the most sites). Sites were chosen by randomly selecting change polygons. These areas were interpreted for change using color aerial photography at a scale of 1:15,840, TM imagery and field data. Because the decreasing and increasing change classes are relative to each other (large decrease has more relative change than moderate decrease), the interpretation of the photo or image was subjective, based on the amount of interpreted change.

Cause Verification

An attempt is made to verify cause on all change areas to understand the impacts and relationships the landscape is experiencing. GIS overlay, fieldwork and photo interpretation are used to determine the causes of change areas. The CDF forest practices database, the USFS stand record system database and the CDF fire history database are overlaid onto the change map to attribute changes caused by harvests, regeneration and wildfires. USFS resource managers interpret change maps by applying local knowledge and fieldwork to identify sources of change on national forest lands. Similarly, IHRMP personnel consult private landowners to identify sources of change in hardwood rangelands. Areas without a causal agent identified through the above processes become the focus of further field efforts and aerial photo interpretation. Despite all these efforts, full coverage of cause verification is not always possible due to the large number of change areas, insufficient information and inaccessible lands.

Results

Total hardwood rangeland area for the project area is approximately 4.7 million acres, with the majority (3.3 million acres) in private ownership. Blue oak woodland, blue oak/foothill pine and montane hardwood WHR types comprise roughly 96 percent of the area. Approximately 463,000 acres underwent some form of change, with 110,000 acres exhibiting a loss in cover and 353,000 acres showing an increase in cover. *Table 3* lists acres of hardwood change by WHR types and ownership. Montane hardwood exhibits the largest acreage of decrease (56,305 acres) and blue oak woodland exhibits the largest increase (170,125 acres). Relative to its area, Blue oak woodland and blue oak/foothill pine have the largest percent of change at 11 percent (2 percent decrease and 9 percent increase).

Figure 3 displays the distribution of detected hardwood cover change by county. The positive acreage numbers represent detected hardwood cover increase and the negative numbers represent detected hardwood cover decrease. Within the southernmost counties, the majority of detected blue oak woodland decrease is in Kern and Mariposa counties, while Fresno and Calaveras have the largest amount of cover decrease in montane hardwood. Fresno and Mariposa counties show a large amount of detected increase within blue oak woodland, while Madera shows large increases in blue oak/foothill pine. Increase in montane hardwood is largest in Fresno County.

Most of the change occurring in the northernmost counties is in detected decreasing classes. Tehama County has the largest amount of cover increase within blue oak woodland and Butte, Nevada and Tehama counties show marked increases in montane hardwood. Hardwood cover decrease within blue oak woodland and blue oak/foothill pine is greatest in Shasta County, while montane hardwood cover decrease is greatest in El Dorado County. The montane hardwood type shows a large amount of cover decrease in all northernmost counties.

Table 3—*Acres of change by hardwood cover type and owner class.*

	National Forest		**Other public**		**Private**		**All owners**	
	Acres	pct	Acres	pct	Acres	pct	Acres	pct
Blue oak woodland								
Large decrease	17	0	10	0	266	0	293	0
Moderate decrease	1,151	0	107	0	2,396	0	3,655	0
Small decrease	4,263	2	969	1	31,771	2	37,003	2
Little to no change	174,806	66	124,057	87	1,292,333	88	1,591,196	85
Small increase	41,368	16	8,337	6	87,703	6	137,407	7
Moderate increase	22,114	8	1,343	1	5,716	0	29,172	2
Large increase	2,097	1	135	0	1,314	0	3,546	0
Non-veg. change	1,728	1	1,418	1	6,642	0	9,788	1
Cloud or shadow	15,473	6	5,646	4	34,810	2	55,929	3
Total	263,018	100	142,021	100	1,462,951	100	1,867,989	100
Blue oak/foothill pine								
Large decrease	52	0	162	0	247	0	461	0
Moderate decrease	267	1	1,027	1	2,057	0	3,352	0
Small decrease	346	1	2,441	2	8,428	1	11,216	2
Little to no change	22,242	62	84,010	74	490,591	87	596,843	84
Small increase	3,064	9	6,867	6	44,626	8	54,558	8
Moderate increase	1,337	4	1,808	2	2,885	1	6,030	1
Large increase	76	0	121	0	203	0	400	0
Non-veg. change	148	0	9,315	8	2,735	0	12,197	2
Cloud or shadow	8,095	23	8,255	7	11,696	2	28,046	4
Total	35,628	100	114,006	100	563,469	100	713,103	100
Montane hardwoods								
Large decrease	719	0	213	0	3,161	0	4,093	0
Moderate decrease	5,121	1	860	0	10,695	1	16,676	1
Small decrease	12,212	2	2,113	1	21,211	2	35,536	2
Little to no change	550,776	81	161,987	82	1,145,813	89	1,858,576	86
Small increase	39,800	6	6,875	3	62,288	5	108,963	5
Moderate increase	13,880	2	2,777	1	7,091	1	23,747	1
Large increase	1,260	0	975	0	992	0	3,227	0
Non-veg. change	1,424	0	914	0	3,435	0	5,773	0
Cloud or shadow	54,463	8	20,811	11	26,052	2	101,326	5
Total	679,654	100	197,526	100	1,280,739	100	2,157,919	100
Total	978,300		453,553		3,307,159		4,739,011	

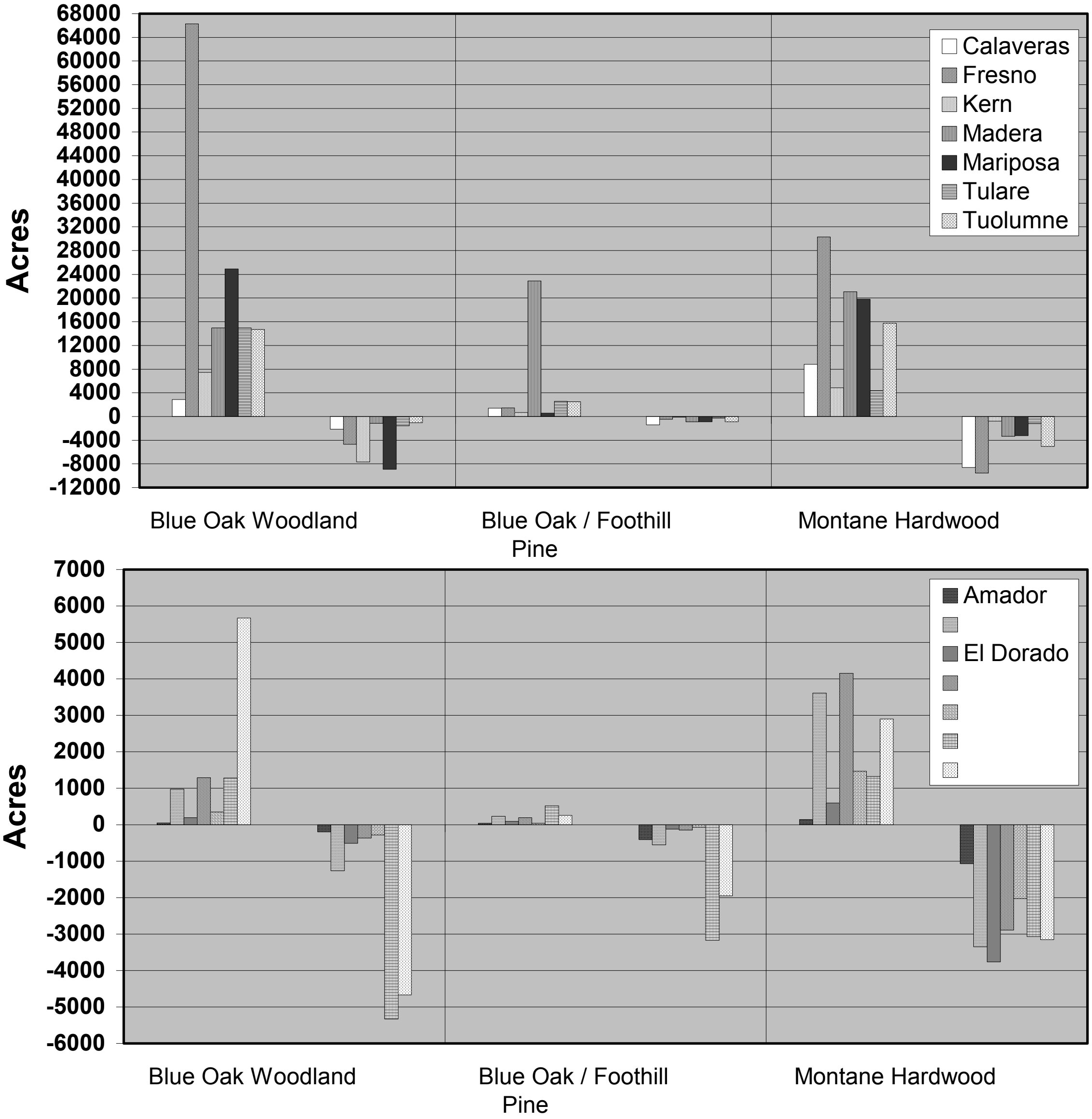


Figure 3—Acres of classified change by hardwood type and county.

The causes of hardwood change by county are displayed in *table 4*. Verified acres represent the total area that has identified cause of change. The acres verified represent change areas that are attributed to some cause. The percentages represent a portion of the total verified acres. The largest cause of change is attributed to wildfire. Harvesting is the largest source of change in Kern, Amador, Butte and Shasta counties. Development or regeneration are major contributors of change in Mariposa, Placer and Tuolumne counties.

Table 4—*Percentage of verified hardwood change by county.*

County	Verified acres	Wildfire	Rx Fire	Harvest	Development	Regeneration	Thinning	Seasonal
		-----Percent-----						
Calaveras	11,962	**49**	5	9	4	24	8	1
Fresno	5,254	**68**	4	1	9	8	10	0
Kern	988	20	27	**41**	0	0	0	12
Madera	3,806	2	10	**45**	10	3	10	19
Mariposa	12,117	10	16	15	5	**49**	3	2
Tulare	723	**62**	0	12	14	0	12	0
Tuolumne	6,095	**67**	0	0	4	26	2	0
Amador	1,362	7	19	**35**	17	0	1	12
Butte	4,475	12	6	**26**	13	14	3	25
El Dorado	1,693	**37**	0	7	23	6	1	13
Nevada	5,422	**68**	0	10	3	7	0	12
Placer	1,036	2	0	24	11	**25**	0	38
Shasta	8,722	29	2	**31**	6	5	16	12
Tehama	10,550	**87**	0	2	4	0	1	7

All images were co-registered using a third-order affine transformation model. Overall root mean square errors of 0.5 pixel to 0.25 pixel were obtained for all image pairs using this model. *Table 5A-C* displays the error matrix for the project area. The overall accuracy of the change map is 89.3 percent. This means that of the 300 sample sites, 268 were correctly classified (the reference and classified classes are the same). Errors of commission (reference class included in the wrong classified class) and omission (reference class excluded from the correct classified class) are also evident. For example, one site is classified as LDVC when the reference class shows it was actually MDVC *(table 5A)*. Therefore, one area was omitted from the correct MDVC class and committed to the incorrect LDVC class. The producer's accuracy of each change class ranged from 67 percent to 100 percent and the user's accuracy ranged from 60 percent to 100 percent *(table 5B, 5C)*. Producer's accuracy represents how well the reference data of each change class is classified. User's accuracy indicates the probability that a given change class actually represents that same change on the ground.

The accuracy assessment also shows how well the methods classify decreases and increases. Areas classified as a decrease were always a decrease, although the correct class was not always assigned. The same is true for the areas classified as an increase. The small decrease and increase classes have sites classified into the little to no change class (8 and 5 out of 45, respectively). This error is expected, however, as this type of change can be very subtle and the methods will have difficulty detecting it.

Table 5A— *Change Map Accuracy Assessment for the Project Area.*

	Reference class								
Classified as	**LDVC[1]**	**MDVC**	**SDVC**	**NCH**	**SIVC**	**MIVC**	**LIVC**	**NVG**	**TOTAL**
LDVC	8	1							9
MDVC	1	12	7						20
SDVC	1	2	30						33
NCH			8	150	5			3	166
SIVC					38	1	1		40
MIVC					2	14			16
LIVC							9		9
NVG								7	7
TOTAL	10	15	45	150	45	15	10	10	300

Table 5B—*Producers accuracy.*

LDVC	8/10	80 pct
MDVC	12/15	80 pct
SDVC	30/45	67 pct
NCH	150/150	100 pct
SIVC	38/45	84 pct
MIVC	14/15	93 pct
LIVC	9/10	90 pct
NVG	7/10	70 pct

Table 5C—*User's accuracy.*

LDVC	8/9	89 pct
MDVC	12/20	60 pct
SDVC	30/33	91 pct
NCH	150/166	90 pct
SIVC	38/40	95 pct
MIVC	14/16	88 pct
LIVC	9/9	100 pct
NVG	7/7	100 pct

[1] LDVC—large decrease in vegetation cover; MDVC—moderate decrease in vegetation cover; SDVC—small decrease in vegetation cover; NCH—little to no change in vegetation cover; SIVC—small increase in vegetation cover; MIVC—moderate increase in vegetation cover; LIVC—large increase in vegetation cover; NVG—non-vegetation change; CLD/SHA—cloud or shadow.

Discussion

The LCMMP produces change data portraying vegetation canopy cover increases and decreases over 5-year time periods. The change classes span a continuum from large decreases to large increases in vegetation cover. These classes are qualitative and represent the diversity found in natural landscapes. Each change class has overlap within and between classes, providing a valuable qualitative assessment of change. A quantitative or categorical assessment offers a more comprehensive representation of change, but requires validation from many ground measurements.

The high accuracies of these data enable the monitoring of hardwood rangelands across large areas. These data easily detect large changes in vegetation cover, such as those resulting from development, harvest and wildfire. They also detect more subtle changes including thinning. Caution must be made because vegetation increases are not always representative of increases in hardwood canopy. In some cases they are related to seasonal variation and successional characteristics, such as growth of grass or shrub following a disturbance. Hardwood types with low canopy cover are particularly sensitive to this phenomenon due to the presence of understory grasses and shrubs.

Identifying the cause of change provides additional information for observing trends over the landscape. Causal information is most easily obtained using available statewide databases, such as fire history and forest practice. Private landowners provide information on activities altering the landscape through IHRMP coordinated workshops. Resource managers can integrate this knowledge into existing policies, maps and plans for a greater understanding of what is occurring on the landscape. This information also may aid in predicting future conditions or determining appropriate management methods.

The IHRMP is one mechanism to promote effective education in assessing voluntary compliance with hardwood resource protection standards, hardwood resource management results and trends in hardwood resource use. Recognizing the value of monitoring data over large areas and its ability to provide various degrees of change, counties have begun to explore the utility of these data. In Fresno County, the change data were presented to private landowners and the Fresno Resource Conservation District as an educational tool for assessing local voluntary guidelines for hardwood rangeland conservation. Napa County, in collaboration with the IHRMP, is assessing the utility of the change data for local planning issues, including identifying changes in riparian and wetland cover, mapping patterns of urban development, locating conversion of agricultural land and open space to urban uses, and monitoring habitat fragmentation. Future efforts focus on analyzing policy issues and trends in land cover over time using these data.

Conclusion

The LCMMP directly addresses CDF's need for a long-term monitoring strategy to inform discussion of issues centered on California's hardwood rangelands. CDF now has the ability to identify trends in hardwood rangeland structure, health, resource use and other factors that affect long-term viability across large regions. The LCMMP provides critical information on the impacts management decisions and natural forces have on the environment. This information includes the actual location and extent of change with respect to the ground, three levels of vegetation cover increase and decrease and the cause of change. Knowing the location and extent of vegetation change provides a picture of the distribution and concentration of change areas. The levels of change give an indication of the severity of vegetation removal or vigor. Understanding what is causing these changes creates an awareness of the impacts change agents have on the landscape.

The LCMMP produces other benefits by providing monitoring data to other agencies, private interest groups and stakeholders. These data can answer the different question these entities may have at different spatial scales. At regional scales, ecosystem characteristics or function can be investigated by examining the cause of change over time, the balance of vegetation increase and decrease, and whether changes are temporary or permanent (e.g., fire versus development). Examining changes in vegetation at a more sub-regional or local scale can help resource managers evaluate the impacts of disturbances on natural resources of local interest. This information is useful to assess the effectiveness of existing policies, programs, management activities and regulations, and to develop alternatives as needed (e.g., county voluntary guidelines for oak woodland management). Finally, these data provide a valuable tool for the IHRMP to work with landowners and state and local governments in resolving hardwood issues.

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Collaborative Monitoring in Walnut Creek, California[1]

Heidi Ballard,[2] Ralph Kraetsch,[3] and Lynn Huntsinger[2]

Abstract

In 1995 and 2000, a monitoring program was designed and implemented to track oak regeneration and native grass populations in target management areas in the four Open Space Preserves of the City of Walnut Creek, California. The program resulted from a collaboration of scientists at the University of California, Berkeley, a group of interested citizens known as the Walnut Creek Open Space Foundation, and the city of Walnut Creek. The goals of the monitoring project were determined by the City and the Foundation, as were the study site locations. The Foundation members volunteered and were trained to collect field data in both the 1995 and 2000 studies. All parties believe that they benefited from this collaboration, sometimes in unexpected ways. The volunteers stated that they learned where they might need to target their oak restoration efforts, and got a better idea of the value and limitations of a scientific monitoring program. The scientists found that they learned about the goals and abilities of local citizens and had to re-examine some of their own assumptions. The City of Walnut Creek managers stated that they gained insight into priorities of Preserve users and knowledge of areas that might require new management efforts.

Introduction

Monitoring, to evaluate changes in condition and/or progress toward meeting a management objective, can take many forms. It may be an integral part of an adaptive management project, a tool to assess changes in the population of a target species, or a means to assess changes in biodiversity (Elzinga and others 2001). Conservation biologists and land managers alike espouse the importance of long-term monitoring to restoration, protection, and natural resource management projects (Holechek 2001, Noss and Cooperrider 1994). In the case of the Walnut Creek Open Space Preserves, the goal was to monitor oak regeneration and native grass populations in specific target areas of interest to the Open Space Foundation. These areas were subject to various management practices, including planting of native grasses, cattle grazing, and cattle exclusion but the study was not designed to experimentally test the effects of these management practices in a broadly generalizable way. Rather, City land managers and Foundation members use the monitoring information to help make decisions about where they should focus

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seedling protection and planting efforts, and if necessary, modify existing practices, in the specific areas targeted for monitoring.

Collaborative management and participatory monitoring projects are based on the notion that conservation and resource management are most effectively executed when local people participate in the management and monitoring of the biodiversity and natural resources (Getz and others 1998). A variety of programs have employed some measure of community involvement in the management and monitoring of the resources they both use and protect: wildlife management programs in Africa put the responsibility of monitoring and management of large game animals in the hands of local people on communal lands (Childs 1996); Masoala National Park in Madagascar was delineated with input from local people who use potentially ecologically sensitive areas (Kremen and others 1998); extractive reserves in Brazil have been operated by cooperatives of rubber tappers who monitor and manage their own resource extraction (Hecht and Cockburn 1989). Though diverse, all of these programs have received attention for the varying degrees of success and limitations they have experienced in achieving their ecological and socio-economic goals (Getz and others 1998, Hannah and others 1998).

Though much of the work on community-based monitoring and management has occurred in regions outside the United States, the many similarities between the issues that these projects face and local land management issues in the U.S. are striking. In both cases, land managers are often in dire need of monitoring information, but lack the funds to get it. Local people, with a variety of interests and experience in a resource area, are often left out of the scientific research and decision-making for the land they know and care about. Finally, in both the U.S. and abroad, scientists are often not aware of the knowledge and concerns of the local people, nor perhaps even those of the land managers. Ironically, scientists, managers, and local people don't often communicate with each other when looking for ways to monitor the effects of management practices. Communication and collaboration between community groups, land managers, and scientists, whether in a game reserve in Southern Africa or an open space preserve in Walnut Creek, California, has the potential to greatly benefit all parties as well as the resource itself. Recent efforts called "all-party monitoring" projects have emerged that involve federal and local agencies as well as grass-roots community groups and environmental organizations (Gray and Kusel 1998). The intention is that collaboration will be more likely to produce an ecological monitoring program that persists due to participation and buy-in, is cost-effective and informative for managers, and provides researchers with a living laboratory and knowledgeable research assistants.

The Walnut Creek Open Space Biodiversity Monitoring Project in 1995 and 2000 was an attempt at just such a collaboration between managers, community members, and scientists. Much of the successes and obstacles encountered in designing and implementing this collaborative monitoring project parallel those experienced in developing countries. On the other hand, some of our experiences were unique to working in a middle- to upper-class city in the San Francisco Bay Area. The process of monitoring oak regeneration in the Walnut Creek Open Spaces is on-going, as a monitoring project should be. However, the lessons learned by the city managers, the community volunteers, and the university scientists may already be useful to other organizations interested in collaborative monitoring projects.

Methods

The Place

The project was conducted in the rolling oak-dominated foothills of eastern Contra Costa County. The City of Walnut Creek manages four Open Space Preserves that total 2,800 acres. Most parcels share borders with larger regional and state parks, but nonetheless are adjacent to the suburban development characteristic of the area. Plant communities on these parcels include blue oak, valley oak, and coast live oak woodlands, and mixed chaparral, riparian and coastal scrub communities, all with annual grasses in the understory. A number of native perennial bunchgrasses are interspersed among the annual grasses, including needlegrasses (*Nassella* spp.), melic grasses (*Melica* spp.), wild rye (*Leymus* spp.), squirreltail (*Elymus* spp.), and others.

The People

The Walnut Creek Open Space Foundation was founded in 1979, and today consists of a group of active citizens who enjoy and have an interest in the management of the oak woodlands, grasslands, and riparian areas of Walnut Creek's four Open Space Preserves. One of their major projects is an Oak Habitat Restoration Project, for which they carry out acorn harvests, waterings, acorn and seedling plantings, acorn storage experiments, and other activities throughout the year. They have an active Board whose members are primarily retired long-time residents of Walnut Creek, and who are often a major source of labor for the Foundation's activities. The City of Walnut Creek Open Space Superintendent is responsible for the management of all four Open Space Preserves, including issuing cattle grazing permits, managing public recreation, maintenance, and management of open space natural resources. The researchers involved in the project are from the Department of Environmental Science, Policy and Management of the College of Natural Resources at the University of California, Berkeley. Extension and outreach is one of the missions of this land-grant institution.

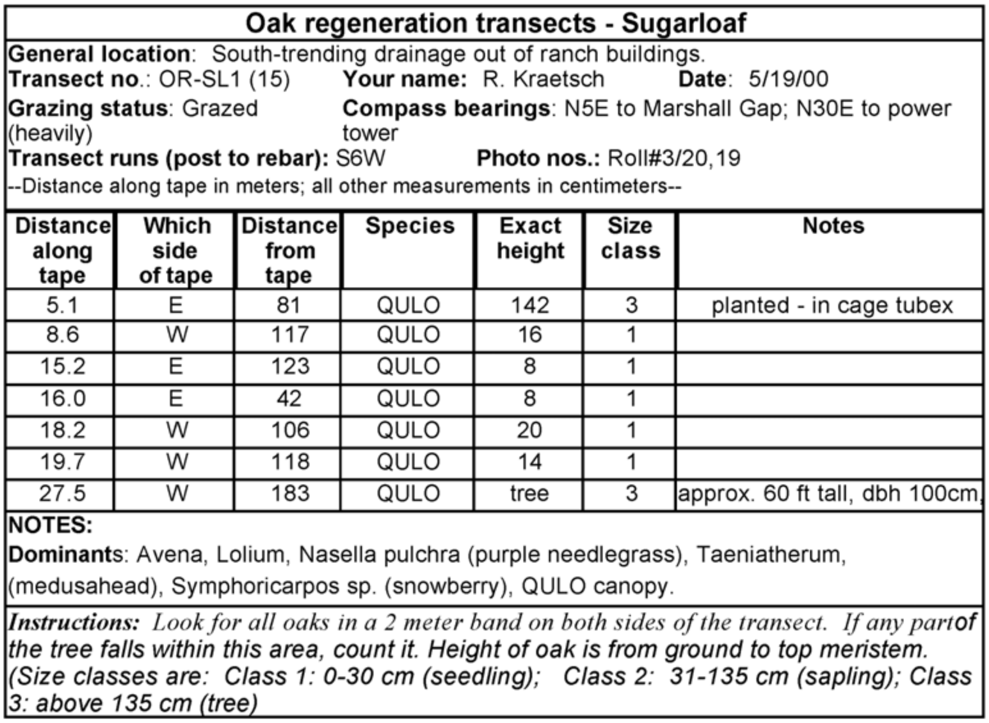
The Process

The Walnut Creek Open Space Foundation has been conducting oak plantings and waterings for several years with the consent and encouragement of the City Superintendent. The City and Foundation wanted to know more about what was happening over time to oaks and native grasses on the preserves. There is, for example, some debate about the impacts of some management practices, particularly livestock grazing. In 1995, the Foundation decided to initiate a monitoring program that would help them assess "…whether the work they were doing was affecting or improving the Open Spaces" (Kraetsch, personal communication), and to evaluate how things were or were not changing in grazed and ungrazed areas. The City Superintendent contacted the College of Natural Resources at the University of California, Berkeley, because he knew that several researchers there specialized in California range and oak woodlands and would improve the quality and credibility of the project.

In order to develop a program that addressed the management objectives of the community and the City, Professor Lynn Huntsinger and her graduate students visited the Preserves with Foundation Board members, learning about their particular concerns and questions regarding management practices: Was the cattle grazing in some areas affecting the regeneration of the oaks? Were the native grass plantings taking hold over the long term? Were the cattle affecting the native grasses? Foundation members identified specific target areas of interest, usually in places where oak seedlings and/or native grasses were already present. These became the locations of the permanent monitoring transects.

The most important factor is that the questions and objectives originated with the Foundation, not the researchers. Designed as a monitoring exercise to indicate progress toward the management goals of the Foundation and City of Walnut Creek, the project's intention was to track changes in special areas within the preserves, and in particular resources, to see if management changes were needed. The researchers provided a reliable yet user-friendly monitoring protocol that addressed stakeholder objectives. If an oak regeneration transect seemed to show poor recruitment, the next step would be to investigate the cause. This might lead to annual monitoring or to testing alternate management. It is up to the managers and stakeholders to develop creative management approaches that incorporate monitoring information.

Because the majority of the monitoring data would be collected by non-ecologist members of the Foundation, researchers designed the monitoring protocol with clear instructions for the users as well as accurate scientific data collection procedures *(fig. 1)*. Foundation members were provided with a reference binder of samples of the native grasses. Foundation volunteers were organized by the Board and trained by the scientists to identify species and take measurements consistently. Oak species in three class sizes were counted and measured on four-meter wide belt transects. Several transects included native bunchgrass abundance and photo points for visual comparison. Data collection occurred during May and June of 1995; re-surveying occurred during May of 2000. In both 1995 and 2000, the researchers compiled and analyzed the data and presented the results in a report to the Foundation and the City.



Oak regeneration transects - Sugarloaf

General location: South-trending drainage out of ranch buildings.

Transect no.: OR-SL1 (15) **Your name:** R. Kraetsch **Date**: 5/19/00

Grazing status: Grazed (heavily) **Compass bearings**: N5E to Marshall Gap; N30E to power tower

Transect runs (post to rebar): S6W **Photo nos.:** Roll#3/20,19

--Distance along tape in meters; all other measurements in centimeters--

Distance along tape	Which side of tape	Distance from tape	Species	Exact height	Size class	Notes
5.1	E	81	QULO	142	3	planted - in cage tubex
8.6	W	117	QULO	16	1	
15.2	E	123	QULO	8	1	
16.0	E	42	QULO	8	1	
18.2	W	106	QULO	20	1	
19.7	W	118	QULO	14	1	
27.5	W	183	QULO	tree	3	approx. 60 ft tall, dbh 100cm

NOTES:

Dominants: Avena, Lolium, Nasella pulchra (purple needlegrass), Taeniatherum, (medusahead), Symphoricarpos sp. (snowberry), QULO canopy.

Instructions: *Look for all oaks in a 2 meter band on both sides of the transect. If any part of the tree falls within this area, count it. Height of oak is from ground to top meristem. (Size classes are: Class 1: 0-30 cm (seedling); Class 2: 31-135 cm (sapling); Class 3: above 135 cm (tree)*

Figure 1—Example of oak regeneration data sheet.

Results and Discussion

At this point in time, after five years with one repeated visit, there were no large changes in oak recruitment and abundance of native bunchgrasses. Because seedlings are ephemeral in the oak woodland, seedlings were not used to evaluate regeneration success. An increase or decrease in the number of saplings, therefore, was used to assess recruitment levels for each transect. Some areas showed an increase in blue oak *(Quercus douglasii)* recruitment into the sapling class in ungrazed areas, whereas valley oak *(Quercus lobata)* had similar recruitment in grazed and ungrazed areas. One of the preserves had a change in grazing management in 1998, from light grazing to ungrazed, which makes conclusions about effects of grazing difficult for that area. In all cases these results are specific to target areas in the Walnut Creek Open Space Preserves.

The experience of implementing the monitoring program with a mix of scientists and non-scientists, students and retired people, rangers and volunteers provided us with a bounty of lessons and recommendations for those who might want to try a collaborative monitoring effort. A crucial element of this process is the art of capitalizing on the strengths of each group in an efficient and respectful way. The Open Space Foundation had monitoring objectives and volunteer labor, but needed outside expertise to establish a monitoring program. The City managers supported the need for monitoring data, but didn't have the personnel, finances, nor time to do the job or hire an outside consulting firm. The university scientists had expertise and were willing to help, but could not provide the quick turnover time that consulting firms are known for. Fortunately, each group participating in the project complemented the needs and constraints of the others.

In many respects, the collaborative effort of the Walnut Creek Open Space project paralleled the efforts of community-based management in other regions of the world. The Foundation volunteers provided a historical and intimate understanding of the landscape that neither the scientists nor the land managers could provide. Though managers and scientists had only recent experience with the area, many of the volunteers have walked these foothills for 40 years. This knowledge was crucial in both the design of the monitoring protocol and in the interpretation of the results in light of the management history. On the other hand, though many of the volunteers had extensive experience with the oak woodlands, they lacked some ecological training. One volunteer explained, "I'm a retired civil engineer. To meet people who could identify a plant with some degree of certainty was like enlightenment to me!" (Ceasar, personal communication). The scientists could contribute their expertise in ecology by designing a protocol that would be repeatable over time, and by analyzing and presenting the results in a way that addresses the management questions. The combination of this scientific "procedural knowledge" and the local "experiential knowledge" resulted in a rewarding learning situation for everyone involved. University participation also provided a "third party" point of view that was useful to volunteers and managers in discussing management options for the preserves.

Participation in the monitoring program provided Foundation members with more than just a new appreciation of plant identification; it gave them a better understanding of the benefits and limitations of the scientific process. Non-ecologists often look to scientists for causal connections or "black and white" answers to management questions, which are difficult to provide in a typical land management setting. Participating in every step of the protocol means that community members are more likely to understand the results, their implications, and can communicate these results to others. In addition, lack of continuity is often an obstacle to long-term monitoring conducted solely by scientists or managers due to limited funding, attrition and movement between institutions. In the case of the Walnut Creek Project, participation by community members will be the single greatest reason that this project continues. As long as Foundation members remain interested and invested in the results of the project, it will continue.

Conclusions

The project report presentation for the 1995-2000 monitoring project reflected the unique circumstances and success of a collaborative project. The researchers gave an informal presentation at the City of Walnut Creek Superintendent's office to several uniformed park rangers and Foundation Board members and volunteers. The volunteers enjoyed scrutinizing the results that had been generated by their days in the field collecting data. The park rangers were delighted to have a body of data from which they could begin to discern the effects of some of their management activities. The scientists found an appreciative yet appropriately critical audience. In fact, the Foundation was so pleased with the work of the researchers that one graduate student received a $200 tip!

The lessons learned do not end with the project report, however. A major criticism of some community-based management and monitoring projects involving scientists or researchers is that they are often "hit and run", that is, once the project is complete, the researcher abandons the community and moves on (Getz and others 1999). This need not always be the case. Since the completion of the 2000 phase of the monitoring project, the relationship has been maintained by a researcher who periodically participates in the oak plantings and watering of the Oak Habitat Restoration Project. There is an un-quantifiable value to researchers and community volunteers working side by side in a continuation of the relationship formed through the monitoring project. However, in the long term, it is the local people who are the most committed to the site for the long term, and who will see that the project continues. Because they participated in the projects design, goals, and implementation, the Foundation is well equipped to do so.

Several aspects of the Walnut Creek Project are very different from the experiences of community-based management projects reported in the literature (Barrow and Murphree 2001). The longevity of this monitoring program will depend on several factors that reflect the unique situation of working with an empowered group of middle-class retirees in the San Francisco Bay Area (*table 1*).

Table 1—*Comparison of obstacles to collaboration in monitoring projects.*

Community-based projects in developing regions	Walnut Creek Open Space Monitoring Project
Often a large power differential; researchers' and community members' education, socio-economic status, ethnicity are dissimilar (Getz and others 1999).	Little to no power differential; researchers' and community members' education, socio-economic status, ethnicity are similar.
Government agencies often unstable—may hinder collaboration (Childs 1996).	Government agencies relatively stable—enables collaboration.
Remote location may not allow for opportunity for collaboration.	Neighboring university allows for opportunity for collaboration.

The largest obstacle in participatory monitoring in developing countries is often a differential in power or status between scientific "experts" and the local community (Barrow and Murphree 2001). In this case, though dichotomies existed between ecologists and non-ecologists, students and retired persons, the Walnut Creek Open Space Foundation Board members knew how to work within the system of governmental agencies and universities and were not intimidated by the prospect of working with researchers. In fact, many of the Foundation members were engineers, geologists and other professionals. The differences in disciplinary training between ecologists and community members contributed more to misunderstandings than socio-economic or cultural differences did. This certainly contributed to the ease with which this project was established and maintained, and will hopefully contribute to its future success. These are presented below.

The Foundation leaders, researchers, and city managers all generated recommendations for non-profit organizations, agencies, and academics that might be interested in pursuing a similar collaborative monitoring project.

- **Land managers and governmental agencies**—When in need of monitoring information without strict time constraints, consider drawing on the resources of the local university. Managers should also keep in mind that different institutions, departments, and researchers have different specialties that may reach far beyond their local area; they can start by asking for help at the local college, and then pursue researchers who may be farther away but specialize in the habitat of interest.

- **Community groups and non-profit environmental organizations**—These organizations should have specific goals and objectives for what they want to monitor and why. Especially when time and money are limited, explicit priorities need to be clearly defined so they can be communicated to the researchers and agency personnel. An important factor that was present in the Walnut Creek Open Space Monitoring Project is organized and strong leadership. When working with university researchers with limited time, it is essential that community groups organize their volunteers efficiently. In addition, make sure there is enough continuity within the organization to sustain the project even after the research support is gone.

- **Academics and natural resource scientists**—Though academics may not consider outreach and extension as part of their typical job description, they should consider contacting local resource management agencies and community groups who may be able to contribute ideas, study sites, labor, and positive public relations toward achieving their research goals. Collaboration can enhance appreciation for local expertise, and promote an exchange of knowledge about the landscape that could not be achieved by science alone. Most importantly, the relationships created can help break down the barriers that often exist between agencies, communities and scientists.

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Inventory of Oaks on California's National Forest Lands[1]

Thomas Gaman[2] and Kevin Casey[3]

Abstract

California has 18+ million acres of land owned by the USDA Forest Service. This is almost 20 percent of the area of the state. From 1994-2000 the Region 5 Remote Sensing Lab collected forest, vegetation and fuels inventory data from thousands of permanent monitoring plots established on diverse sites on Forest Service lands throughout the region. The plots are stratified among 165 vegetation types, or strata. Collectively, these data are known as the Regional Forest Inventory and Analysis (FIA) database. An analysis of the plot data for California's oak, including species, distribution and stocking is presented. These wildlands are rich in many species of oak. Based upon the FIA survey, there are 433 million (+/– 1 percent) oak trees over 5 inches in diameter on Forest Service lands in California. Eleven percent of all trees on the Region 5 ownerships are species of the genus *Quercus* or *Lithocarpus*. They can be expected to be encountered on 87 strata which collectively occupy 11.5 million acres of land. Sixty-three strata, together comprising 6.6 million acres, have combined average oak basal area greater than 5 square feet per acre.

Introduction

The Region 5 Remote Sensing Laboratory of the USDA Forest Service (USFS), in accord with directives of the National Environmental Policy Act and the 1998 Farm Bill, collected consistent forest, fuels and vegetation inventory data from a sampling grid of cluster plots throughout the National Forest lands in California. This program is known as Regional Forest Inventory and Analysis (FIA). The Region 5 FIA database for California, completed in 2000, is the only extensive, systematic and consistent region-wide dataset of its kind. The database is available to the public in compiled and raw formats and is useful for a wide variety of vegetation survey and data analysis applications.

Methods

Data were collected across the landscapes on all forest types at 18,435 sample point locations on approximately 3,800 "cluster plots." Each 1-hectare cluster plot includes four to five sample point locations. At each point vegetation cover type, tree data, understory vegetation data, and duff/woody debris data were recorded. A global

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[1] An abbreviated version of this paper was presented at the Fifth Symposium on Oak Woodlands: Oaks in California's Changing Landscapes, October 22-25, 2001, San Diego, California.

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positioning system (GPS) location was collected at the center point of each plot where possible. Once completed, quality control teams of experienced foresters and biologists visited a random sample of more than 10 percent of the plots to assure accurate data collection. Detailed methodology is described in the Region 5 FIA Field Manual (USDA 1999).

USFS Remote Sensing Lab (RSL) personnel assigned vegetation type strata labels to every sample point. The strata labeling is based on CALVEG, a vegetation type map developed from LandSat Thematic Mappper data (30 meter) using image processing techniques developed at RSL, Boston University and San Diego State. In forested strata the overall vegetation cover types were further refined via aerial photo interpretation, field data interpretation, and ground verification. For conifer types strata labels were assigned which consist of a Regional CALVEG Type label, a crown size class label and a density designation (USDA Forest Service 2001). For hardwood, shrub and other non-forest types the first letter of the stratum label characterizes the vegetation form (shrub, tree, rock, etc.), and the latter two letters are the CALVEG type code (USFS 2001, see *table 1* footnote). Overall accuracy of the final maps was determined via an independent accuracy assessment. One hundred sixty-five strata distributed over 18,555,998 acres were identified by the USFS image processing and mapping team. There is a direct crosswalk between Wildlife Habitat Relations (WHR) and CALVEG labels and so the stratified maps and field data can be used in both contexts.

Based on the mapping team's efforts, we used the geographic information system (GIS) database to calculate total acreage for each of the 165 strata. Thirty-two of these strata comprise less than 10,000 acres each and, together, they make up less than 0.75 percent of the land area. These strata were removed from the analysis because of high standard errors resulting from low sample size. Another 131,000 acres of lakes was removed from the sampling area, leaving a total of 18,297,000 acres made up of 132 strata listed below *(table 1)*. Together they include 99.25 percent of Region 5's land ownership.

Table 1— *The 132 selected strata with acreage of each.* [1]

Stratum	Acreage	Stratum	Acreage	Stratum	Acreage
A2P	41,545	I3G	85,308	P4P	25,643
A3N	174,328	I3N	12,842	PNO	27,583
A3P	226,572	I3X	31,847	R2N	23,743
A3S	83,783	IQC	417,714	R2P	43,119
A4N	14,967	IQD	88,724	R3G	89,617
AXX	28,460	IQG	76,583	R3N	399,754
C3N	26,786	IQQ	21,174	R3P	151,765
C4N	35,135	IQW	48,437	R3S	23,326
D2N	36,208	J2S	12,073	R4G	99,258
D2P	36,439	J3G	13,193	R4N	138,363
D3G	211,768	J3N	130,323	UAX	152,115
D3N	334,314	J3P	150,674	UBA	753,917
D3P	211,060	J3S	38,158	UBB	41,525
D4G	549,975	J4G	24,303	UBS	626,036
D4N	273,039	J4N	46,994	UDX	177,356
D4P	43,966	J4P	49,887	UGR	46,259
D4S	21,284	K2N	34,581	UHG	170,721

(Table 1 continued)

Stratum	Acreage	Stratum	Acreage	Stratum	Acreage
D5G	42,641	L3G	16,019	UHJ	30,175
D5N	38,587	L3N	146,429	USB	136,805
E2N	83,625	L3P	40,938	USS	86,250
E2P	120,142	L3S	40,473	W2N	10,857
E3N	324,729	M0X	10,127	W3G	29,866
E3P	148,680	M2N	103,648	W3N	131,558
E4N	23,884	M2P	67,045	W4G	36,491
E4P	32,714	M3G	268,913	W4N	83,919
F2G	10,356	M3N	385,551	XC1	24,016
F2N	90,621	M3P	91,497	XCM	140,415
F2P	41,774	M3S	35,317	XCV	33,120
F3G	283,750	M4G	495,981	XCX	310,964
F3N	769,972	M4N	295,068	XNO	299,825
F3P	148,447	M4P	54,536	ZAX	15,675
F3S	13,835	M4S	28,243	ZBB	102,104
F4G	385,210	M5N	20,087	ZBL	144,662
F4N	279,152	MNO	45,526	ZBM	107,653
F4P	13,095	N2N	76,609	ZBS	412,762
FNO	10,584	N2P	156,329	ZCA	303,720
H2G	40,113	N2S	60,864	ZCC	190,604
H3G	80,040	NPJ	710,226	ZCD	20,694
H3N	26,474	P2P	11,949	ZCH	78,959
H3X	18,145	P3G	52,471	ZCQ	1,570,426
HQK	152,234	P3N	150,149	ZCR	86,614
HQT	61,904	P3P	124,066	ZCS	57,370
I2G	89,149	P4G	82,492	ZCT	66,746
I2N	114,262	P4N	48,869	ZCZ	98,519

[1] **Key to Strata Labels:**

1. First digit: Regional CALVEG Type Label (for all strata)

A alpine
C coulter pine
D Douglas-fir
E eastside pine
F eastside mixed conifer
H hardwood (productive)
I hardwood (non-productive or shrub)
J jeffery pine
K knobcone pine
L lodgepole pine
M westside mixed conifer
N pinyon-juniper
P ponderosa pine
R red fir
U non-forest
W white fir
X shrub type (productive)
Z shrub type (non-productive)

2. For Conifer and Commercial Hardwood Strata:

Second digit: Size Class 0=seedling, 1=sapling, 2=small poles, 3=small sawtimber, 4=large sawtimber, 5=very large sawtimber

Third digit: Density Class 0=1-10 percent canopy cover S = 10-25 percent P= 25-39 percent
N = 40-59 percent G = 60+ percent

3. For non-productive Hardwood and Shrub Strata:
No size class and density is provided. The second and third letters are the CALVEG type labels (USDA Forest Service 2001).

Data for all trees greater than 5 inches diameter at breast height (dbh) were extracted from the statewide database. Raw data were broken down into 132 separate strata for analysis. Stratified data were then processed to yield number of live trees per acre and the basal area for all species encountered. We further calculated the basal area by position (Dominant, CoDominant, Intermediate/Suppressed), the standard error of the total basal area for each stratum, and the standard error of the overall mean. A summary was created for each stratum, with estimates of variance, and coefficient of variation. Because the statistical summaries for some of the individual strata revealed some standard errors in the 12-20 percent range, all 18,000+ sample points distributed across the landscape were pooled to estimate total tree number of oaks by species, and the overall oak population.

Results

Although forest characteristics within a single stratum may indeed vary considerably due to diverse geographic, edaphic, ecological and climatic conditions, stratification provided a good means to calculate the statewide USFS oak population from real plot data evenly distributed and sampled from stands throughout each regional stratum.

Trees of all sizes were measured during the inventory and are available within the Region 5 FIA database. However, only those trees ≥5 inches in diameter at breast height are considered in this report. Therefore, this analysis ignores the shrub oak populations, which are very common in the Southern California chaparral types.

Community associations of different oak species growing together are found at many sites. Ten types (1.15 million acres) support combined oak populations with basal areas of 50 square feet per acre and greater.

Black Oak

Black Oak (*Q. kelloggii*) appeared as greater than 5 percent of the stand basal area in 40 of the 132 types, together comprising 4,321,000 acres or 25 percent of Region 5 Forest Service lands. Although USFS has 152,000 acres of forest lands classified as a black oak stratum (HQK) it never represents more than 50 percent of the basal area in any stratum. In the HQK type black oak accounted for only 29 percent of the basal area, 27 percent by number of trees, and 52 trees per acre. On 939,000 acres of land black oak is greater than 20 percent of the total basal area. The overall stratified estimate is that there are 105 million (+/– 5.1 percent) black oak trees greater than 5 inches in diameter growing on California's Forest Service lands *(fig. 1).*

Canyon Live Oak

Canyon live oak (*Q. chrysolepis*) is the most widely distributed oak on Region 5 lands. It occurs as more than 5 percent of the stand by basal area in 54 of the 132 strata, together occupying 6.9 million acres or 40 percent of Region 5 lands. In 21 types together occupying 2.3 million acres of land this species comprises greater than 20 percent of stand basal area. There are 417,000 acres of a hardwood canyon live oak type averaging 72 canyon live oaks and 29 black oaks per acre. In addition canyon live oak is abundantly represented in Southern California chaparral types, as an understory species on the west side of the Sierra Nevada and throughout the coast range (accounting for the very high "seedling" or advance regeneration count in this species). The inventory showed an overall population of 212 million (+/– 3.8 percent) canyon live oak trees ≥ 5 inches dbh (*fig. 2*).

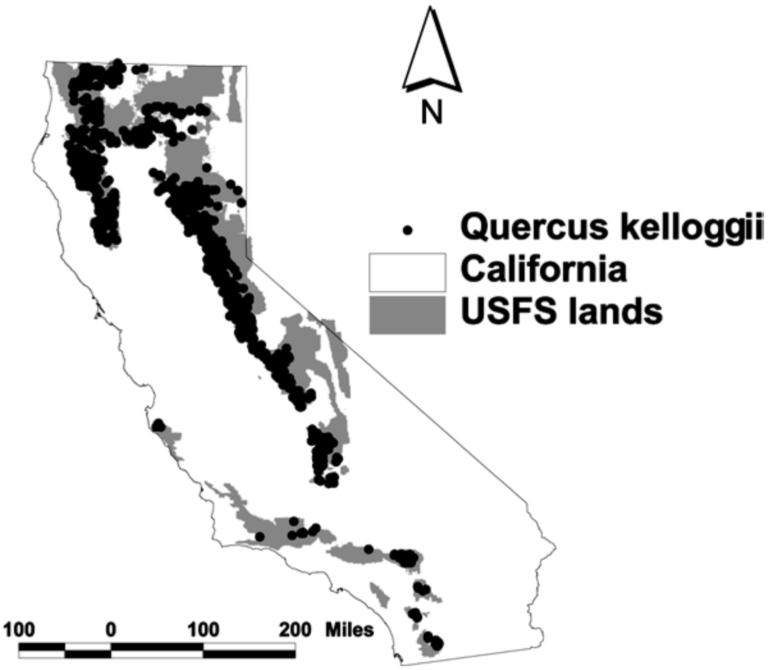

Figure 1—Black oak on USFS lands.

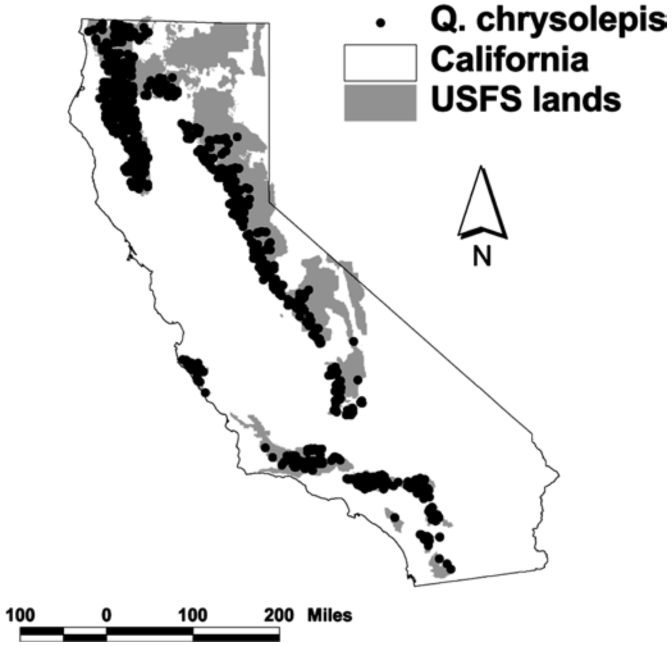

Figure 2—Canyon live oak on USFS lands.

Interior Live Oak

Interior live oak (*Q. wislizenii*) is less widely distributed on Region 5 lands with an overall population of 20 million (+/– 11.4 percent) trees. There are 8 strata, totaling 1.17 million acres, where interior live oak represents greater than 5 percent of the total basal area and only a single type (IQD) of 88,000 acres where there is a basal area of more than 10 square feet per acre of interior live oak. The IQW type (48,000 acres) has a basal area in that species of only 6.5 square feet per acre. The species is mostly found with canyon live oak, blue oak, and black oak. It is rare in conifer stands (*fig. 3*).

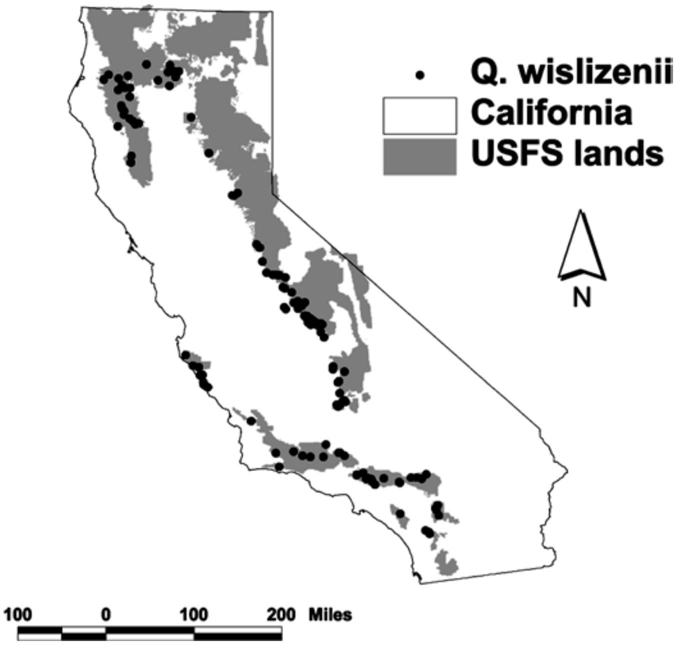

Figure 3—Interior live oak on USFS lands.

Oregon White Oak

Oregon white oak (*Q. garryana*) forests occur sporadically in the IQG type on 76,000 acres of the project area, all in the north coast. Oregon white oak accounts for more than 5 percent of the basal area in 4 strata, together totaling 273,000 acres. There are also thickets of the shrub form, known as Brewer oak (*Q. garryana* var *breweri*), coded as brushlands, on the Sierra and Sequoia National Forests in the Southern Sierra, and in the northern Coastal Range forests. This species extends north throughout Oregon, Washington and into British Columbia. Interestingly Oregon white oak occurs very sparsely in a great variety of forest types in northern California. The stratified inventory yielded 24.5 million trees (+/– 11.4 percent, *fig. 4*).

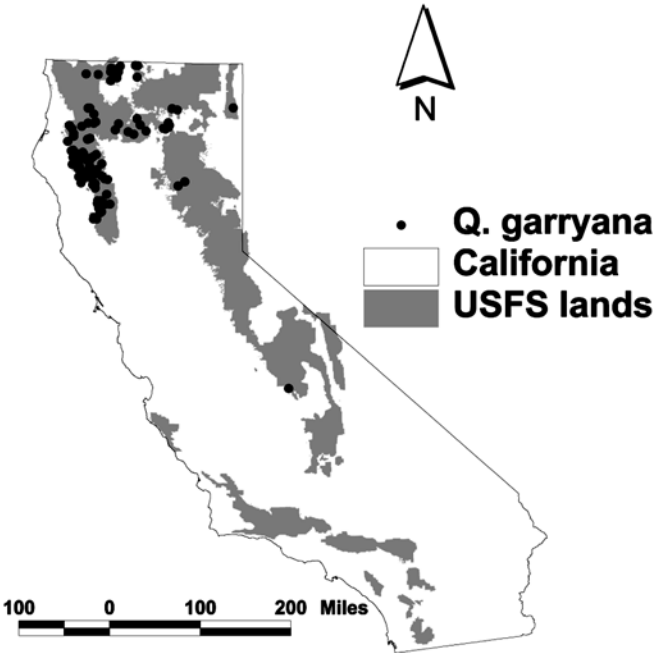

Figure 4—Oregon white oak on USFS lands.

Tanbark Oak

Tanbark oak (*Lithocarpus densiflorus*) forests occur at lower elevations on the Plumas and Tahoe National Forests where there are 62,000 acres in the hardwood stratum HQT. In all there are 11 strata, together totaling 928,000 acres of land, where tanbark oak is greater than 5 percent of total basal area. Tanbark oak also occurs as a shrub in the understory of a large variety of coniferous forest types. Tanbark oak occurs in far greater abundance along the more coastal areas of northern California, where 100 percent stands of this species occur frequently. There are some such stands on USFS lands in the lower elevation forests of the Plumas National Forest in the Feather River basin near Oroville. In those locations the high density of tanbark oak is such that, although relatively minor in extent, there is an overall population of 59.5 million trees (+/– 15.4 percent >5 inches dbh, *fig. 5*).

Blue Oak

Blue oak (*Q. douglasii*) is common on ranch lands in the Central Valley and adjacent foothill woodlands. The species does not reach significantly onto Forest Service lands, where it is very rare. The Forest Service owns 88,000 acres of lands classified as blue oak woodland, located mostly in the lower Kings River and San Joaquin River basins. There are 48,000 acres of land classified as an interior live oak type (IQW) where blue oak is a minor component. Blue oak is also sparsely represented in isolated patches in some of the chaparral types. The stratified inventory yields 5.3 million trees (+/– 14.8 percent, *fig. 6*).

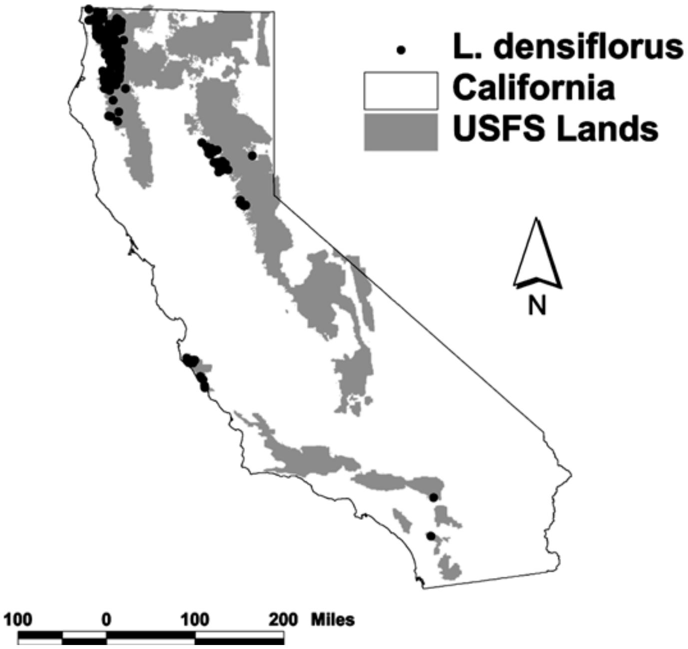

Figure 5—Tanbark oak on USFS lands.

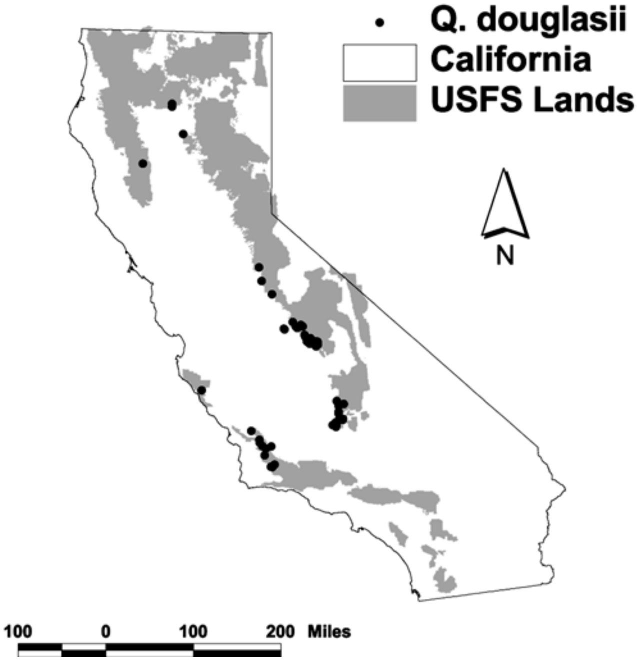

Figure 6—Blue oak on USFS lands.

Coast Live Oak

Coast live oak (*Q. agrifolia*) comprises more than 5 percent of the basal area on 7 woodland strata which together occupy approximately 342,000 acres. Of that, the species is sparsely represented in the southern and central California chaparral and coastal scrub (Los Padres National Forest) on 201,000 acres of open and canyon hardwood lands characterized by low basal area. These are the I2G, I3G, and C3N types where coast live oak basal area varies from 10-23 square feet per acre. Coast live oak is a very minor component of an additional 1.12 million acres within 8 other chaparral and conifer strata, mostly on the southern California National Forests, where it occurs sporadically in clumps less than one hectare in size, below the size of the minimum mapping unit. The inventory yielded 6.5 million trees (+/– 14.2 percent >5 inches in dbh, *fig. 7*).

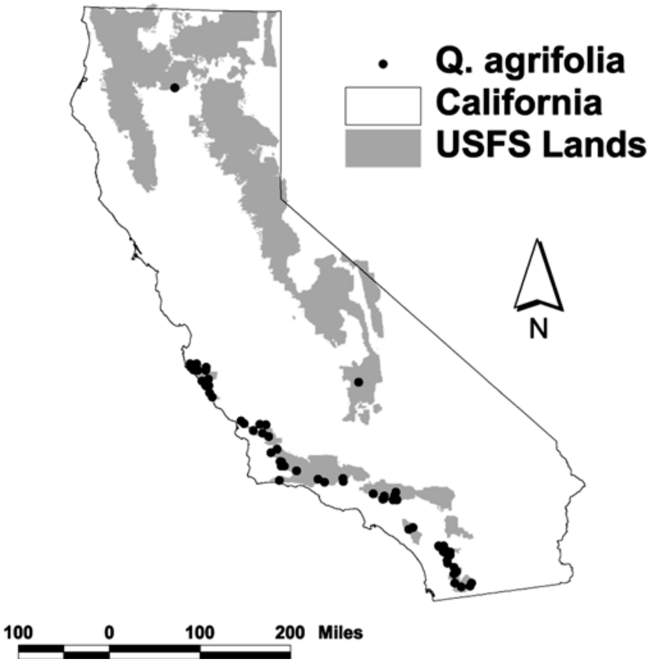

Figure 7—Coast live oak on USFS lands.

Crown Position

Black oak, canyon live oak and interior live oak are often observed crowded among faster growing conifers, where they are gradually losing access to direct sunlight. By basal area 12 percent of these trees were in dominant positions relative to their immediate neighbors in the stand while 61 percent were co-dominant and the remaining 27 percent were intermediate or suppressed. By comparison, when white fir, incense cedar and sugar pine (the most shade tolerant species and low to mid-elevations) were evaluated, 34.6 percent of those trees were in dominant positions and 45.6 percent more were in co-dominant positions. These data suggest that oaks may be struggling to retain their vigor in stands where they grow among the more aggressive conifers. Shade tolerant conifers such as white fir (*Abies concolor*) and incense cedar (*Calocedrus decurrens*) in mixed conifer stands, and invasive Douglas-fir (*Pseudotsuga menziesii*) in oak woodlands, seem to outcompete oaks of all species. This is most likely due to fire suppression and a changing climate, which is yielding hotter, moister years throughout the Region, probably not favoring oak species.

The Census

Overall, oak trees over 5 inches in diameter can be expected to be encountered in 87 strata together comprising 11,552,000 acres, or almost 2/3 of California's national forest lands. Because oak trees were sampled infrequently on many of these strata, the standard error of the basal area estimate had high variance in some of the strata with very minor oak populations. However, there are 63 strata with combined average oak basal area greater than 5 square feet per acre, together comprising 6.66 million acres of Region 5 lands. The overall oak population (of trees 5 inches and larger) on those lands is 394,422,000 trees with a weighted by basal area average of 9.8 inches dbh. When the data are processed on a non-stratified basis (e.g. all the plots combined and processed as a unit) they show a total oak population also of 433 million oak trees (*fig. 8*). This estimate has a standard error of 3.0 percent. This indicates that, although stands are highly variable, the more than 18,000 sample points create a stratified inventory of high precision when queried for aggregate population estimates.

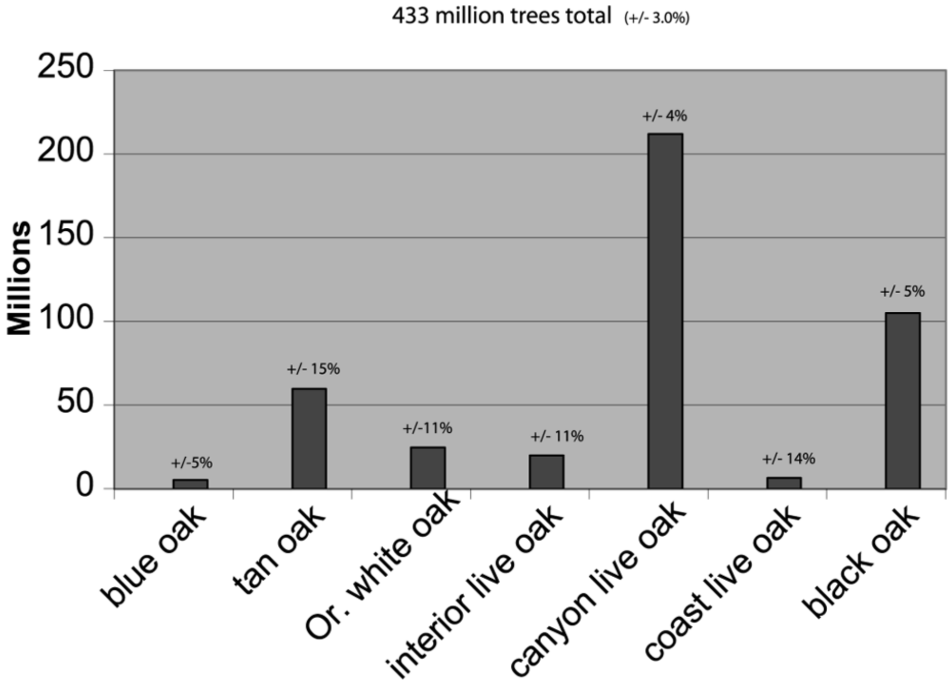

Figure 8—Number of oaks >5 inches dbh on USFS Region 5 lands.

Diameter Distribution

Processing the data by diameter class reveals that 18.5 trees per acre, or 74.2 percent of the oaks, are in the 5-10 inch diameter classes *(fig. 9)*. A further 5.6 trees, or 22.7 percent are, in the 10-20 inch diameter classes. In the larger size classes 2.5 percent of the trees, as measured by number of trees (not by basal area) are in the 20-30 inch classes. A tiny fraction (0.5 percent) is in the 30+ inch group. This is the typical J-curve; however, it falls off exceedingly rapidly, indicating the importance of preserving large oak trees in our native California forest.

When the data are processed by species the oak trees range in average diameter, weighted by basal area, from 8.8 inches (interior live oak) to 13.9 inches (coast live oak).

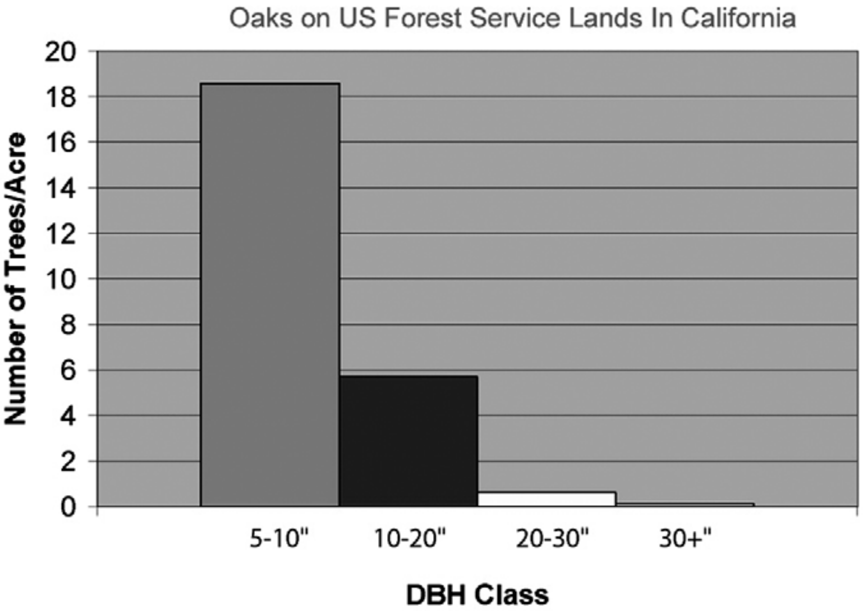

Figure 9—Oak diameter distribution.

Largest Trees

Analysis of the data shows that the largest trees actually measured during the inventory project were as indicated below:

Species	Max DBH (inches)
Black oak	60.6
Coast live oak	68.8
Canyon live oak	68.0
Interior live oak	39.2
Oregon white oak	54.2
Tanbark oak	50.5

Regeneration

Combining regeneration data across the entire region confirms our field observations that oak regeneration, while highly variable, is very common in the forest understory. Most abundant are canyon live oak with an average of 57 trees (less than 1 inch in diameter and greater than 6 inches in height) per acre and California black oak with an overall regeneration of 28 trees per acre. Both of these species range throughout California's National Forestlands except in the high Sierra and the east side types. Regeneration of other species was encountered irregularly. Having visited thousands of these survey points, it is clear to us that that there is abundant "advanced regeneration" of oak seedlings that can respond to fire or other canopy removing events.

Comparisons with Other Inventories

The Pacific Northwest Research Station (PNW) conducted independent inventories of private lands in California in the 1990's (Waddell and Bassett 1997). Although their figures are published only for timberland by county groupings known as "Resource Areas," the data are readily consolidated in a spreadsheet. A review of that inventory for black oak and canyon live oak (by far the most abundant oaks) on private timberland in 3 applicable Resource Areas (totaling 40 California counties) indicates an estimate of 142 million oak trees on 4.7 million acres, or just over 30 oaks per acre. That estimate is consistent with our estimate (25 trees per acre) as presented here considering the fact that the 18+ million Forest Service acres of our review area includes non-stocked and poorly stocked shrub lands, generally of lower site, that were not included in the PNW "timberland" inventory.

Summary

This report generalizes oak populations for Forest Service lands in California where oaks account for 11 percent of all the trees. This analysis does not consider tree ages, smaller oak trees or shrub types. Further regional analysis of the FIA oaks data is certainly necessary. More detailed analysis of oaks or other species by forest, ranger district or other area can be generated using ForestServer shareware by Gaman (2000).

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Monitoring Conservation Success in a Large Oak Woodland Landscape[1]

Rich Reiner,[2] Emma Underwood,[3] and John-O Niles[4]

Abstract

Monitoring is essential in understanding the success or failure of a conservation project and provides the information needed to conduct adaptive management. Although there is a large body of literature on monitoring design, it fails to provide sufficient information to practitioners on how to organize and apply monitoring when implementing landscape-scale conservation projects. We describe a decision framework currently being developed by The Nature Conservancy. It can be used to help set monitoring goals, prioritize monitoring efforts, and select monitoring metrics. Monitoring goals should be organized around at least three purposes. First, they should be closely tied to each specific conservation action and measure progress in implementing that activity. Second, monitoring should measure the impact the strategy has on abating its targeted threat. Third, the measures should test and validate the assumptions made regarding how the natural community functions. We provide examples of how these three types of monitoring are being applied to a large blue oak woodland landscape in the Lassen Foothills of northern California.

Introduction

Monitoring, the repeated measurement of variables over time and space, is an essential component of understanding the eventual success or failure of any conservation project. It also provides the foundation for an adaptive management approach to project activities (Christensen and others 1996). The act of monitoring in the context of conservation projects, however, is both complex and multi-faceted. It could include measures which provide information on threats, the condition of conservation targets, legal compliance, and testing hypotheses about how an ecosystem functions. Monitoring projects in large landscapes are further complicated by the fact that they occur within and across complex ecological systems with multiple anthropogenic threats. Consequently, more than a single conservation strategy is often employed in an attempt to abate those threats.

Although there is abundant literature regarding monitoring methods (Elzinga and others 1998, Thompson and others 1998), a significant challenge for conservation practitioners working in large landscapes is the design of efficient and affordable monitoring programs which can assess progress towards achieving

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[1] An abbreviated version of this paper was presented at the Fifth Symposium on Oak Woodlands: Oaks in California's Changing Landscape, October 22-25, 2001, San Diego, California.

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conservation goals. We propose that monitoring programs have the highest chance of success if they arise from a well-organized conservation plan and continually provide feedback to managers. Given that there are few examples of successful monitoring programs and a much larger number of failures (Gibbs and others 1999, Yoccoz and others 2001), we describe a decision framework which can be used to help project managers set monitoring goals, prioritize monitoring efforts, and select monitoring metrics in a large landscape scale project. This framework is based on ideas being developed by The Nature Conservancy (TNC) as they attempt to design a monitoring framework to support TNC's emerging Conservation by Design methodology (TNC 2000, 2001). We present some of these ideas, and illustrate their current or anticipated application (presented in boxes) to a large oak woodland conservation project in the Lassen Foothill region of Tehama County, California.

Study Area

Blue oak (*Quercus douglasii*) woodland is a biologically rich and widespread vegetation community found primarily in the western foothills of the Sierra Nevada, the southern Cascade, the eastern foothills of the Coast Range and the Transverse Range (Barbour and Major 1988, Standiford and Tinnin 1996). Despite its vast spatial extent, the landscape's rolling topography and proximity to valley urban centers has focused development pressure in the blue oak woodlands. Additionally, most of this woodland occurs on private ranch land which is increasingly being subdivided for housing or converted to vineyards and orchards. This trend is encouraged by poor returns in the cattle industry and by aging ranchers passing monetarily valuable properties to heirs with other interests. Unlike California's conifer forests, few large blue oak woodlands are protected within public parks or other conservation ownerships.

The Lassen Foothills oak woodland covers approximately 300,000 acres and is surprisingly intact, primarily because of large private cattle ranch ownerships. The woodland occurs on rocky volcanic soils, and the oaks vary in density from sparse savannas to thick groves. The shrub layer is spotty over much of the landscape and is mostly composed of *Ceanothus cuneatus* and manzanita's *Arctostphylos sp.* The ground layer is predominantly non-native annual grasses mixed with native and introduced forbs. Native perennial grasses such as *Nassella pulchra* and *Aristida sp*. are present, but are found only in small scattered patches. Troublesome non-native species which have become common in the region include medusahead (*Taeniatherum caput-medusae*) and yellow starthistle (*Centaurea solstitialis*). Wild fires and grazing are important processes in the landscape. Fires occur most often during the hot dry summer months, while cattle graze the woodland from October to late May.

Conservation by Design

Developing a monitoring plan for a complex project becomes easier if the conservation approach is clearly organized. The Nature Conservancy uses an approach called *Conservation by Design* to select and plan its projects (TNC 2000). TNC's vision is to conserve a portfolio of functional conservation areas within and across ecoregions. We define ecoregions as relatively large units of land containing a distinct assemblage of natural communities and species. Site selection within ecoregions is an iterative process built around five steps:

- Identifying the species, communities, and ecological systems within the ecoregion;
- Setting specific goals for the number and distribution of these conservation targets to be captured in a portfolio of sites;
- Assembling information and relevant data on the location and quality of conservation targets;
- Designing a network of conservation areas that most effectively meets the goals;
- Selecting the highest priority conservation areas in the portfolio for conservation action.

The ultimate selection of conservation strategies is made by:

- Identifying the most serious stresses (threat) impacting the viability of the conservation target and its supporting ecological systems;
- Understanding the sources or causes of the stress;
- Developing an array of actions necessary to abate the threats.

The process outlined above was used to set a goal of preserving at least two large blue oak woodlands in the Northern Sacramento Valley ecoregion and the Lassen Foothills was identified as one of those sites in 1995 (TNC 1995).

In the Lassen woodlands the major known threats in order of severity were determined to be: home development and land conversion to vineyards and orchards, invasion of non-native species, and alteration of the fire and grazing regimes leading to a change of vegetation composition and structure. Even though development is not occurring in this region as quickly as in other areas, it was placed first because it is a threat that is irreversible.

Three primary conservation strategies and quantitative goals have been developed to abate or reduce the threats listed above:

- Conservation easements are being purchased from willing sellers to prevent development, vineyards, transfer of water, commercial woodcutting, and mineral extraction. A goal of up to 165,000 acres of conservation easements has been set.
- A prescribe fire program has been implemented to reduce medusahead and starthistle. A goal of 10,000 acres per year burned and 200,000 acres under fire management has been set.
- Grazing programs are being implemented to fence 20 miles of riparian habitat, and to establish a 6,000-acre grassbank (reserve) to encourage ranchers to rest private rangeland after prescribed burns.

Monitoring Conservation Success

One component of TNC's Conservation by Design initiative involves establishing Measures of Success (TNC 2001). Measures of Success provides a foundation on which to develop conservation project monitoring programs, however, to date TNC has not been able to implement a comprehensive, system-wide monitoring protocol. To this end, we have distilled some of the emerging ideas being considered by TNC and present them in the context of the Lassen Foothills Project.

Once conservation strategies and goals have been selected, monitoring should be organized around at least three purposes:

- First, monitoring should be closely tied to each specific conservation action and measure progress in implementing that activity;
- Second, monitoring should measure the impact of the conservation action (i.e., is the action reducing the identified threat?);
- Third, because conservation strategies are often based on assumptions of how the project's ecosystem functions, monitoring should test and validate those assumptions, inform adaptive land management and establish some long-term indices of ecological health.

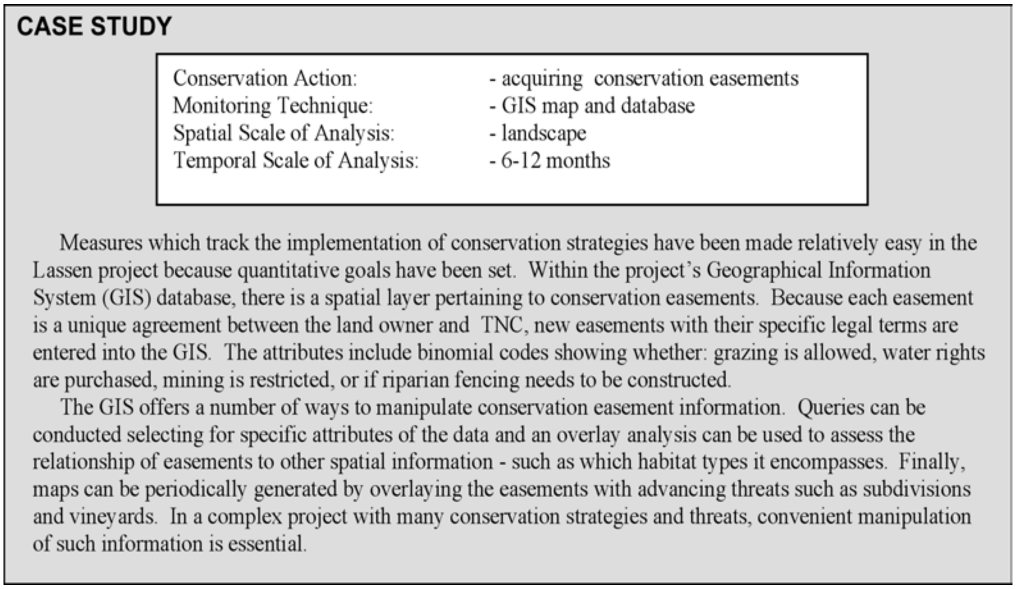
Presented below is a discussion of the types of monitoring which address these three purposes. For each type we present a case study from the oak woodland community of TNC's Lassen Foothills Project to further illustrate feasible monitoring techniques.

Monitoring that Evaluates Conservation Actions

This type of monitoring enables a project manager to assess his or her performance in implementing the specific conservation activities which characterize the project. This should not be confused with measures of how the conservation strategies are working to abate the identified threats (discussed next). The purpose here is to simply track and assess the progress of getting strategies implemented. The results are used to help steer annual planning objectives and operate in a relatively short time span. These results, often in the form of maps or graphs, are also critical to communicate progress internally within an organization and externally to funding partners. Too often the results of monitoring are undermined, or even wasted, if they are not presented in a clear and easily digestible format and in a timely manner. *Figure 1* gives an example of this type of monitoring.

Monitoring that Evaluates Threat Abatement

In order to monitor the ability of a particular conservation action to abate threats, the project manager must be able to track the extent and severity of the threat. These measures often need to occur over a longer time scale than monitoring the implementation of conservation actions. *Figure 2* provides an example of how monitoring can be used to assess the prescribed fire program's ability to abate weeds. Although the indicator of a successful strategy in this case might be a reduction in the target non-native species, monitoring activities should also consider what is replacing these species, thereby providing additional information on the many feedback loops that exist in the ecosystem.



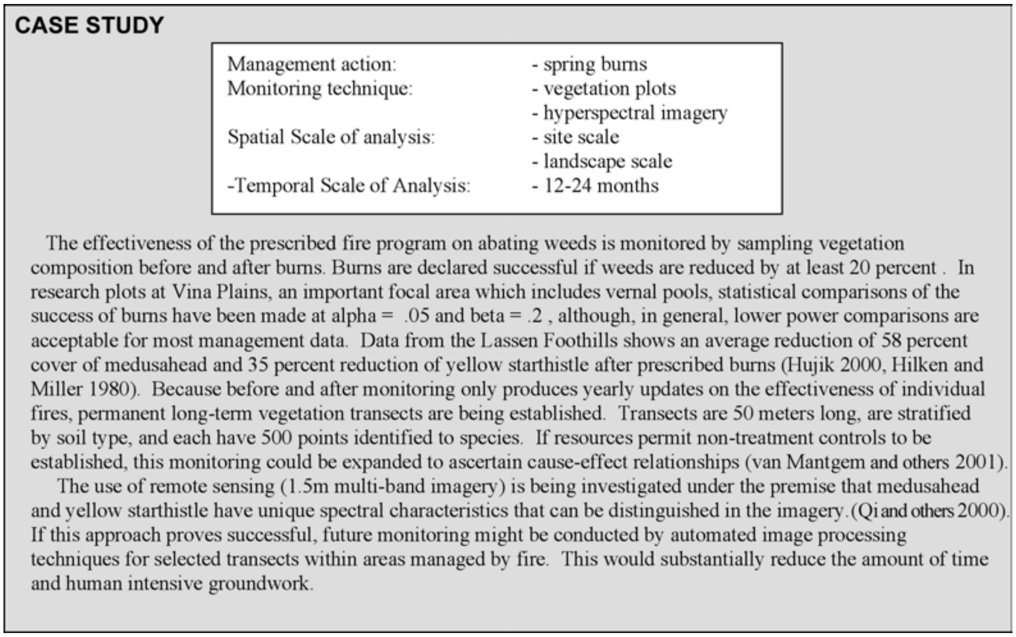
CASE STUDY

Conservation Action: - acquiring conservation easements
Monitoring Technique: - GIS map and database
Spatial Scale of Analysis: - landscape
Temporal Scale of Analysis: - 6-12 months

Measures which track the implementation of conservation strategies have been made relatively easy in the Lassen project because quantitative goals have been set. Within the project's Geographical Information System (GIS) database, there is a spatial layer pertaining to conservation easements. Because each easement is a unique agreement between the land owner and TNC, new easements with their specific legal terms are entered into the GIS. The attributes include binomial codes showing whether: grazing is allowed, water rights are purchased, mining is restricted, or if riparian fencing needs to be constructed.

The GIS offers a number of ways to manipulate conservation easement information. Queries can be conducted selecting for specific attributes of the data and an overlay analysis can be used to assess the relationship of easements to other spatial information - such as which habitat types it encompasses. Finally, maps can be periodically generated by overlaying the easements with advancing threats such as subdivisions and vineyards. In a complex project with many conservation strategies and threats, convenient manipulation of such information is essential.

Figure 1—Monitoring the implementation of a conservation easement program in the Lassen Foothills.



CASE STUDY

Management action: - spring burns
Monitoring technique: - vegetation plots
- hyperspectral imagery
Spatial Scale of analysis: - site scale
- landscape scale
-Temporal Scale of Analysis: - 12-24 months

The effectiveness of the prescribed fire program on abating weeds is monitored by sampling vegetation composition before and after burns. Burns are declared successful if weeds are reduced by at least 20 percent . In research plots at Vina Plains, an important focal area which includes vernal pools, statistical comparisons of the success of burns have been made at alpha = .05 and beta = .2 , although, in general, lower power comparisons are acceptable for most management data. Data from the Lassen Foothills shows an average reduction of 58 percent cover of medusahead and 35 percent reduction of yellow starthistle after prescribed burns (Hujik 2000, Hilken and Miller 1980). Because before and after monitoring only produces yearly updates on the effectiveness of individual fires, permanent long-term vegetation transects are being established. Transects are 50 meters long, are stratified by soil type, and each have 500 points identified to species. If resources permit non-treatment controls to be established, this monitoring could be expanded to ascertain cause-effect relationships (van Mantgem and others 2001).

The use of remote sensing (1.5m multi-band imagery) is being investigated under the premise that medusahead and yellow starthistle have unique spectral characteristics that can be distinguished in the imagery. (Qi and others 2000). If this approach proves successful, future monitoring might be conducted by automated image processing techniques for selected transects within areas managed by fire. This would substantially reduce the amount of time and human intensive groundwork.

Figure 2—Monitoring the effects of prescribed fire on exotic weeds.

Monitoring that Validates Ecological Models

Because our perception of threats are most often based on assumptions of how the ecosystem functions (i.e., reduced grazing leads to increased oak survival), it is important to utilize monitoring as a means of validating these assumptions. The development of a visual conceptual model is a useful way to organize relationships between various components of an ecosystem. These models can ultimately help guide the selection of variables for monitoring. Models are an efficient way to describe the pathways that lead from causes (including management actions) to outcomes (such as a more desired or a less desired ecological condition) (Manley and others 2000, Yoccoz and others 2001). Consequently, models take monitoring a step beyond simply identifying pattern and provides management with information on the underlying mechanisms.

One way to characterize relationships in a natural community is to break it into components and then describe the relationship between those components. Franklin and others (1981) propose to divide communities into three components; composition (species diversity), structure (vertical and horizontal pattern), and function (ecological and evolutionary processes). Alternatively, Davis (1993) suggests beginning with an exhaustive list of system elements (e.g., species, processes) and a description of their relationships. *Figure 3* illustrates a merging of these two approaches for the blue oak woodland of the Lassen Foothills (Allen 1990, Swiecki and Bernhardt 1998).

On the left side of the diagram are three components of the ecosystem; structure, composition, and function. Nested within each of these components are loosely assigned elements of the oak woodland. For example, birds can be considered an element in the composition of blue oak woodlands (e.g., acorn woodpeckers are recognized as a keystone species) (PRBO 2000). The box to the right of this reflects Davis's (1993) recommendation of listing the various attributes of the ecosystem that could be monitored for that element. For example, in the case of birds, surveying for snags and cavities could help supplement more intensive, and costly, bird surveys.

A model such as *Figure 3* is obviously a simplification of the ecosystem: realistically it should include the complex web of one- and two-way relationships between attributes that are related. For example, fire has a feedback loop to ecosystem vegetation—in particular to non-native species. *Figure 4* expands that portion of the model and portrays it as a set of state variables linked by a web of relationships. Some of the relationships are well know, others are not. For example, the relationship between "medusahead thatch increasing with lack of fire, causing natives to decrease" has been well established and does not require further research (Hilken and Miller 1980). However, the relationship between "an increase in native grass and forbs leading to greater oak and shrub survival" is less certain (Keeley 1975, Swiecki and Bernhardt 1998). The latter should be a high priority for research and should be incorporated into monitoring designs. *Figure 5* provides an example of testing of a conceptual model hypotheses within a monitoring program.

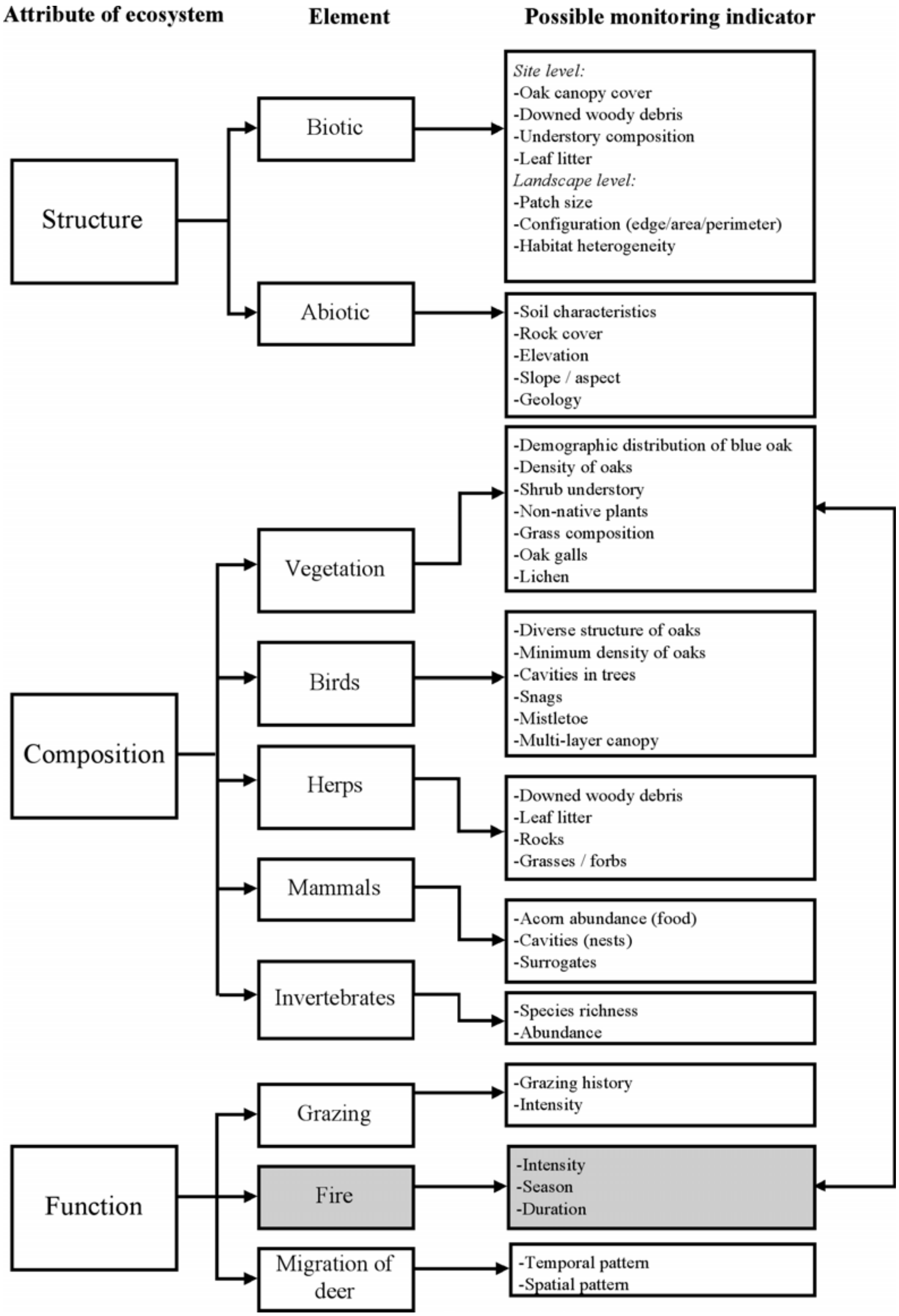


Figure 3—Conceptual model of some components of a blue oak woodland.

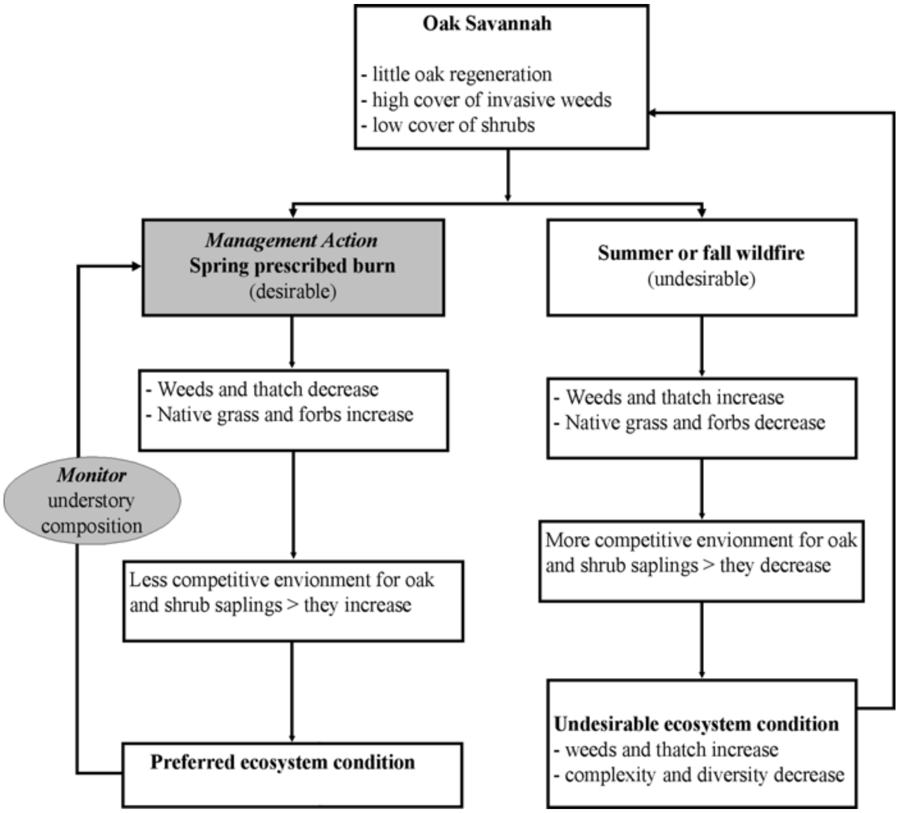
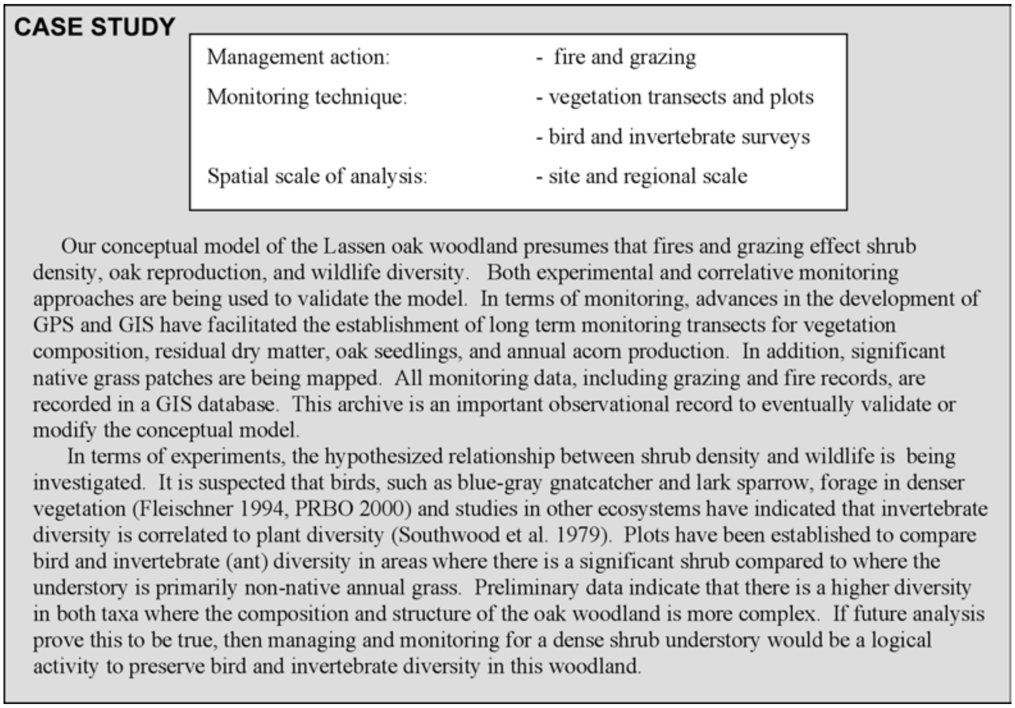


Figure 4—Conceptual model of fire impacts on non-native plants: management action and monitoring.



CASE STUDY

Management action:	- fire and grazing
Monitoring technique:	- vegetation transects and plots - bird and invertebrate surveys
Spatial scale of analysis:	- site and regional scale

Our conceptual model of the Lassen oak woodland presumes that fires and grazing effect shrub density, oak reproduction, and wildlife diversity. Both experimental and correlative monitoring approaches are being used to validate the model. In terms of monitoring, advances in the development of GPS and GIS have facilitated the establishment of long term monitoring transects for vegetation composition, residual dry matter, oak seedlings, and annual acorn production. In addition, significant native grass patches are being mapped. All monitoring data, including grazing and fire records, are recorded in a GIS database. This archive is an important observational record to eventually validate or modify the conceptual model.

In terms of experiments, the hypothesized relationship between shrub density and wildlife is being investigated. It is suspected that birds, such as blue-gray gnatcatcher and lark sparrow, forage in denser vegetation (Fleischner 1994, PRBO 2000) and studies in other ecosystems have indicated that invertebrate diversity is correlated to plant diversity (Southwood et al. 1979). Plots have been established to compare bird and invertebrate (ant) diversity in areas where there is a significant shrub compared to where the understory is primarily non-native annual grass. Preliminary data indicate that there is a higher diversity in both taxa where the composition and structure of the oak woodland is more complex. If future analysis prove this to be true, then managing and monitoring for a dense shrub understory would be a logical activity to preserve bird and invertebrate diversity in this woodland.

Figure 5—Monitoring to validate conceptual models on the impacts of fire and grazing.

Additional Ways to Prioritize Monitoring

It is likely that, even after using a selection framework as described above, the number of proposed monitoring projects will still be more than is possible to implement. To further prioritize projects, monitoring should be subjected to additional filters.

"Cost" is always a consideration, and much of the cost of monitoring is determined by the sampling intensity required to detect significant change. Because the power to detect change in a statistical design is inversely related to the magnitude of the system's variability (Hayes and Steidl 1997), it is important to conduct pilot studies. For example, in the Lassen foothills grasslands perennial plants generally exhibit less year-to-year variability than annuals. After a specific monitoring metric is selected, further increases in statistical power or economy of sampling can be obtained by stratifying samples to reduce variability (for example, concentrating sampling within one soil type or range of elevation). Other methods of increasing statistical power without increasing the sampling intensity and cost include nesting samples at different spatial scales, optimizing the shape of the sampling units, and implementing data handling procedures which minimizes recording errors (Gibbs and others 1999, Steele and others 1984). Also, sampling intensity may be reduced by considering an increase in the alpha (chance of error) and beta levels in which the statistical tests are conducted (Kendal 1992).

Another method to reduce costs is to consider selecting "indicators" which are related in a known way to other environmental conditions. Umbrella species (a species that needs such large habitats that saving it will automatically save many other species) and keystone species (species whose activities have an impact disproportionate to their abundance) should be considered (Karr 1987, Noss 1990). If possible, data could be collected which would serve duplicate purposes. For example, imagery might be used to detect invasive plants as well as identify changes in land-use.

The prioritization of monitoring also should consider the project's "investment" in different conservation strategies. Monitoring should be directed towards the most expensive conservation strategies, whether expense is interpreted as financial, human-power, or time. In the Lassen Foothills the greatest expense is undeniably the purchase of conservation easements where millions of dollars have been expended to date. The long term success or failure of these easements in protecting the viability of this woodland will be known only through monitoring.

Monitoring variables which directly relate to "ecological relationships" which can be manipulated should be considered a priority. For example, in the Lassen woodlands there is some control over timing and frequency of fire though the prescribed burn program. It is thus important to understand how fire impacts the woodland's native biodiversity. On the other hand, we have little control over global climate change. Even though climate change may ultimately be a major threat, it is not within our project's control and thus should receive a lower priority for monitoring.

"Collaboration" with other institutions already collecting and archiving information offers valuable information for project monitoring. We surveyed the literature and looked for other organizations collecting data in the Lassen Foothills region that potentially could be useful for the project. *Table 1* shows some of those monitoring programs.

Integrating outside data into a monitoring program can be challenging as metadata regarding the monitoring programs of others maybe difficult to obtain. Understanding the limitations and assumptions of the data often requires personal visits with researchers. Regardless, the benefits of using others' data most often outweighs the disadvantages. For example, the California Department of Forestry has undertaken a state-wide land use change detection program Fire and Resources Assessment Program (FRAP) which highlights, at a landscape level, changes in the cover of oak woodland which have occurred in the Lassen region each five years. Since this program measures change at the landscape scale, our project does not need to replicate this expensive monitoring and can focus its efforts on elucidating the mechanisms responsible for this change at a finer scale.

Table 1—*Some organizations already collecting data on the Lassen woodland site.*

Type	By whom	Data	Web site
Landscape images and coverages	CA Dept. of Forestry & Fire Protection	Fire and Resources Assessment Program	http://frap.cdf.ca.gov/
	CA Dept. of Fish and Game	California Wildlife Habitat Relationships Information Data Base	http://www.dfg.ca.gov/whdab/html/cwhr.html
	Center for the Assessment and Management of Forest and Environmental Resources	Fire history mapping	http://camfer.cnr.berkeley.edu/
	U.S Geological Survey	California Gap Analysis	http://www.biogeog.ucsb.edu/projects/gap/gap_home.html.
Wildlife surveys	CA Dept. of Fish & Game	Deer counts	http://www.dfg.ca.gov/hunting/part2.pdf
	CA Dept. of Fish & Game	Nocturnal animal counts	N/A
	Point Reyes Bird Observatory	Bird surveys	http://www.prbo.org/
	U.C. Hastings Natural History Reserve	Statewide acorn surveys	http://www.hastingsreserve.org/OakStory/OakIntro.html
Water	CA Dept. of Water Resources	Stream flow	http://cdec.water.ca.gov/

Conclusion

The scientific literature abounds with rigorous methodology designed to monitor and quantify change over time. Yet most long term monitoring programs associated with conservation projects have failed. Most fail because they have not been closely tied to specific goals and thus do not provide timely adaptive feedback to project directors. If the information generated is not immediately useful, monitoring projects quickly become fiscally unsustainable. We have illustrated in this paper a step-by-step guide for linking monitoring to specific conservation project goals, and have demonstrated how to prioritize monitoring in a large blue oak woodland landscape.

To be effective, a monitoring program must provide sufficient information to allow project managers to practice adaptive management and determine the success or failure of their projects. Only through monitoring will we be able to correct past mistakes and be able to truly know the long-term value of today's conservation efforts.

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Historical Oak Woodland Detected through *Armillaria mellea* Damage in Fruit Orchards[1]

Alan K. Brown[2]

Abstract

The wholesale destruction of oak woodland by North American settlers in the Santa Clara Valley is attested in early county histories and other sources. Early plats and field notes by government and private surveyors, which are the most useful kind of sources as to the distribution and extent of the lost oak groves, still leave serious gaps in our knowledge. A further source of information is the dangerous legacy left behind in the soil by the original groves when they were chopped and the roots left to rot. The honey fungus or oak root fungus (*Armillaria mellea*) became a serious problem to the orchard industry in the early twentieth century. Upon vertical aerial photography made at a time when the valley was almost entirely under mature prune and apricot orchard cultivation, a sample 144-km^2 strip was chosen that shows clear cases of highly localized patterns of weakening of the fruit trees, typically in rings and circles of various sizes and ages. These patterns, and the percentages of the surface that they occupy within 25-ha blocks, were plotted on two maps along with any indications of the presence of former oak woodland and/or oak savanna that could be found in historical records. These graphic comparisons between two sorts of information—visible fungus damage and historical evidence of presence of oak trees—give a generally consistent picture that seems useful for filling in gaps in our information, even though a number of precautions have to be observed and some further verification is possible. Further comparisons with soil types or other conditions are also possible, and for similar landscapes, such a use of historical aerial photography may be helpful in delineating the former oak woodlands.

Introduction

The historic extent of native oak groves in central and northern California is rather poorly documented, despite their past economic and even political importance. In 1769, the first Spanish exploring expedition to reach the Santa Clara Valley named it the *llano de los Robles*, the White-Oak level, “a large plain…entirely grown over with white oaks—large ones, and ones of all sizes—and a few live oaks” (Crespí 2001: 603; cf. Stanger and Brown 1969: 103). The well-known description of the English navigator George Vancouver’s visit to Mission Santa Clara from San Francisco in 1792 was calculated to attract the ambitions of non-Spanish nations. Key phrases were: “a country I little expected to find in these regions… [like] a park which had originally been planted with the true old English oak;… [with] the stately lords of the forest in complete possession of the soil”; “an imaginary park…requiring only to be adorned with the neat habitations of an industrious people” (Vancouver 1984: 718, 720). A generation later, another English party on the same route repeated the comparison to a British “nobleman’s park” (Beechey 1968: 44–45). Only a year after that, a French sea captain, while traveling through the same “immense grove of splendid oaks mixed with several other mature trees,” daydreamed of his native land’s ancient Gaulish “druidesses” (priestesses of the oak), but he also coveted the

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[1] An abbreviated version of this paper was presented at the Fifth Symposium on Oak Woodlands: Oaks in California’s Changing Landscape, October 22-25, 2001, San Diego, California.

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contorted timber for shipbuilding purposes (Duhaut-Cilly 1999: 128). Fifty years further on, with the country now in North American hands, a guidebook for railroad travelers spoke of "the great oaks" that "add an indescribable beauty to this country, and grow in great profusion, particularly on the Murphy Grant" (present-day Sunnyvale; Crofutt 1878–1879). Yet the destruction had already been in progress for many years: in the Santa Clara Valley south of Palo Alto "squatters got early possession, and stripped the count[r]y side of the magnificent timber that adorned it, to sell for cord wood and charcoal" (Alley & Bowen 1883: xii).

More focused sources of information are scattered and hard to find. Notorious for the vagueness of their descriptions are the land-grant records stemming from the Mexican period, together with later court testimony and surveys relating to these private claims. Originals of most of the Spanish-language rancho records are in the U. S. National Archives, while copies of varying quality and some originals are held in land-case legal records at the Bancroft Library, Berkeley, and elsewhere. A designation of an area as *roblar* (white-oak grove) must indicate that deciduous oaks were conspicuous there, although not necessarily as the dominant species, and not impossibly only as a savanna. Descriptive names such as *roblar del Torotal*, meaning "the buckeye-patch white oaks," which occupied the area around the present I-280 and I-880 interchange in San José (Lewis 1857 and related records), and *roblar del Yedral*, "poison-oak-patch white oaks," located perhaps in present Menlo Park and East Palo Alto (Osio 1853), add some further information as to the composition of the individual groves. The great band of mixed white-oak and live-oak trees that extended from present Mountain View toward Santa Clara and thence toward Saratoga was designated as "the Roblar" even in American times. Many of these trees were cut down at an early date, although not before the edge of the Roblar had provided a principal call for the boundary of the Rancho Quito land grant (*fig. 1*).

Surveyors' records made in the early American period, comprising field notes and plats of public township and private land-grant tracts, are perhaps the most essential sources of information as to early conditions. Field notes, because of their inherent accuracy, are usually preferable to plats that were drawn up from them. However, for a crucial part of the area examined in this paper, the basic earliest maps exist only in extremely reduced, poor copies, and field notes made in 1866 for township section divisions are lacking (U. S. Surveyor General 1851 *et seq.*: Township 7 South, Range 2 West, Mount Diablo Base and Meridian).

To the above types of historical evidence may be added one more possible resource. During a large part of the twentieth century, fruit orchards filled the Santa Clara Valley from edge to edge, completely replacing such native oak groves as had remained after the earlier losses. Damage to the orchardists' trees from the oak root fungus or honey fungus, *Armillaria mellea*, was quite often believed to be connected with the vanished oaks. "Removing the tops of [oak] trees with infected roots frequently results in the fungus colonizing the whole root system and thus infesting a large area" (Raabe 1970: 133). As early as 1925, it was reported that "The belief has long been held among growers [in the Santa Clara Valley] that so long as its native host [the oak] is alive, the fungus does not leave it to attack fruit trees.… After the death of [the oak] the disease spreads throughout the dead or dying roots." Locally, "It is not difficult to find… authentic cases where the disease has developed in areas from which oak trees had been removed many years before" (Hendrickson 1925: 2-3). "The owner of [one] orchard still remembers the approximate location of the oak

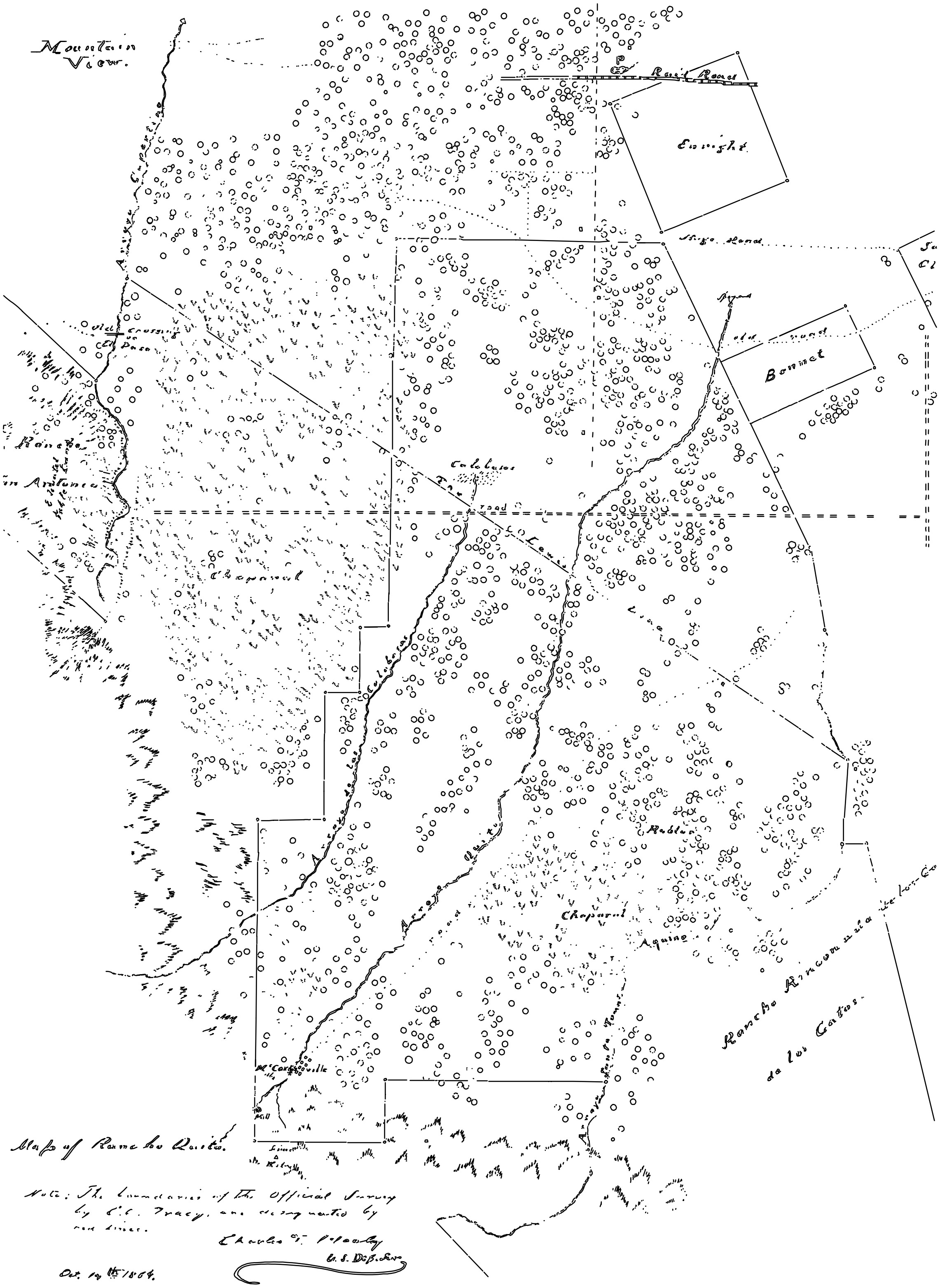

Figure 1—An early map (Healey 1864) indicating oak woodland (circles) and brush (**V**-like symbols) between Mountain View, Saratoga (McCartysville), and Santa Clara. Scale approximately 1:77,000 at page-size reproduction. Orientation is due north.

trees which were cut down more than 30 years ago. In some cases the location of these oaks apparently coincides with what seems to have been the beginning points of the disease in the orchard.… Other infected areas developed in various places and gradually spread until they came together to form one large diseased patch." The location described in this quotation (Hendrickson 1925: 6–8) appears to have been the Stockle (Stocklmeier) property on Stevens Creek.[3] Within the vast and almost uniform extent of the former orchards as shown on early vertical aerial photography (U. S. Agricultural Stabilization and Conservation Service 1939, scale 1:20,000), the evidence of areas ravaged by spreading fungus disease is clearly visible in patterns of bare ground in the form of rings, circles and patches of nearly all sizes, conspicuously interrupting the regular grid of planted trees.

Method

From prints of these aerial photographs, the outlines of denuded patches evidently caused by oak root fungus are simply and easily plotted. For this study, I chose a zone approximately 16 km long by 9 km wide, lying along the western side of the northern Santa Clara Valley roughly between Stevens Creek on the northwest and the old channel of Los Gatos Creek on the southeast. This area seemed suitable for study because there have been almost no trees left in it within the last century and there is historical evidence, but not much detailed information, as to their former considerable extent and importance. The smallest features that seem worth plotting are circular ones with a diameter of about 20 m, evidently representing a fungous patch that has spread so as to affect five adjacent fruit trees at their standard linear spacing of slightly less than 7 m. The circles that have expanded beyond this size tend to touch, overlap, and merge as they grow, and although many of the largest features are slightly less well defined or are somewhat eccentric, almost all of the clearings can still be clearly visualized as rings, sometimes even concentrically nested rings, and their centers often are defined by more or less circular patches of replanted or recovering orchard trees. The patterns are easily traced and plotted upon an adjusted background, and then can be further superimposed upon a graphical interpretation of available historical information (Healey 1863; Healey 1864; Hermann 1879; Howe 1851; Lewis c1850; Lewis 1850a; Lewis 1850b; Lewis 1857; Lewis 1861; Preuss 1849; Stratton 1865; Stratton 1866a; Stratton 1866b; Reed 1866a; Reed 1866b; Tracy 1853; Tracy 1859; U. S. Surveyor General 1851 *et seq.*; United States v. Mary Ann Bennett 1868; Van Dorn 1854; Wallace 1858; Whitcher 1861) concerning the distribution of oak woodland, oak savanna, and chamisal (mixed brush) (*fig. 2*). The sources do not consistently distinguish between oak woodland and oak savanna as these are now defined (Allen-Diaz and others 1999: 324-326), and although terms such as "scattering" are found quite regularly, it is not always clear whether, before the time of any given survey, an area of woodland might not have been turned into something like a savanna through timber cutting. Therefore, a generalized symbol covering both types of oak growth is needed, in addition to the symbol used for clearly attested woodland. In most areas it is not possible to give an exact plotting of borders of either woodland or savanna, and overall the limited and unreliable nature of the sources must be recognized.

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[3] Information provided from History/San José (San José Historical Museum) office by Paula Jabloner, archivist.

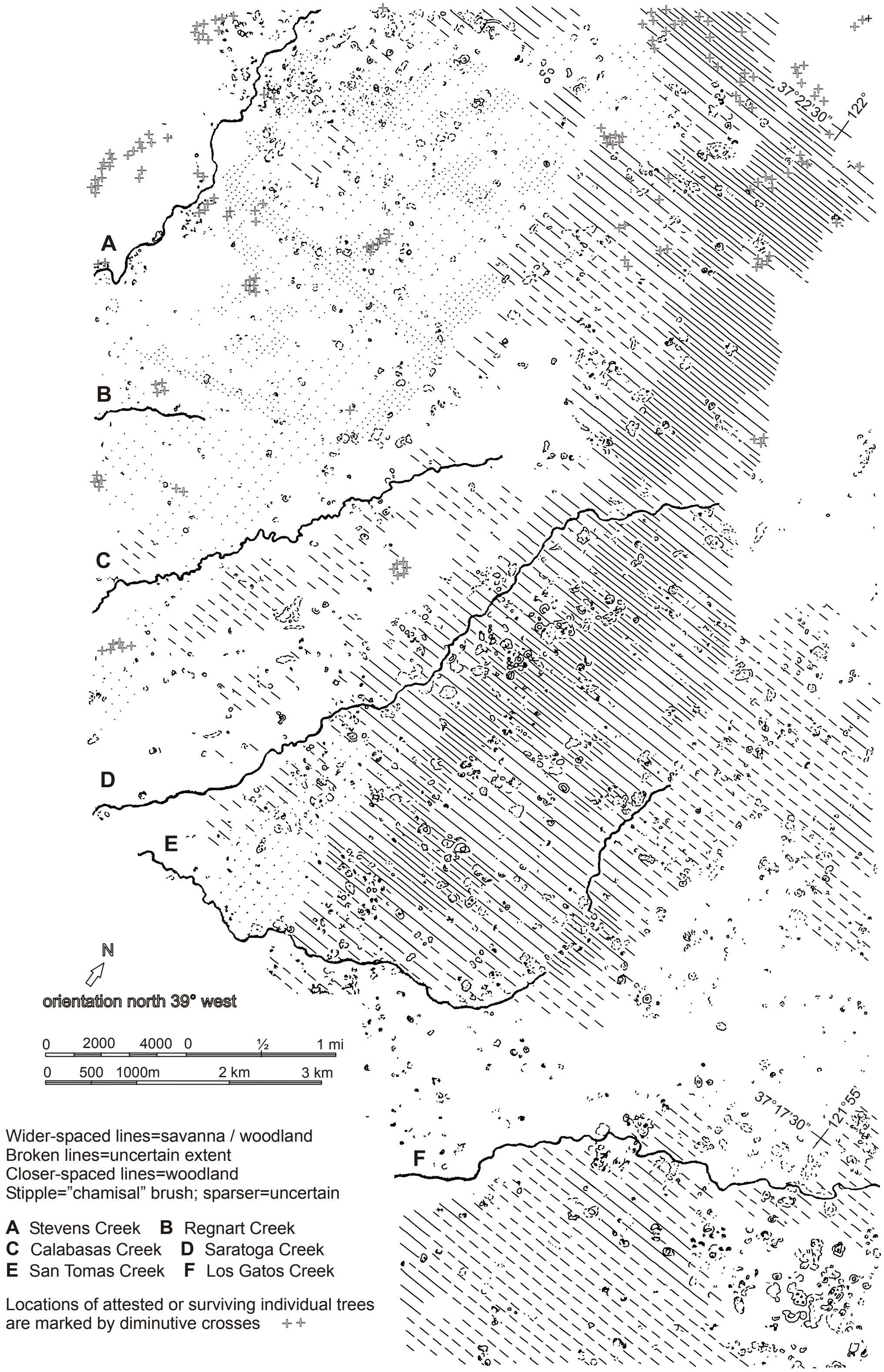

Figure 2—Oak root fungus damage in orchards, interpreted from vertical aerial photographs (U. S. Agricultural Stabilization and Conservation Service 1939. Scale 1:71,250 at page size.

In order to provide some numerical indication of the amounts of apparent fungus damage, the area was divided into squares measuring 127 m on a side (approximately 1.6 ha), within each of which the percentage of its area occupied by orchard marks was estimated, and these results have been summarized by plotting some 517 one-half-kilometer-square (25 ha) blocks marked according to percentage ranges of the areas of their surfaces occupied by affected patches (*fig. 3*). Historically known, although only very approximately locatable, outlines of the Roblar, and of the large body of brush and live oak within it known as the Chamisal (e.g., Beardsley 1926; Tracy 1859; Welch 1931: 257, 262), are added for comparison.

Discussion

Since the available historical evidence, sparse and unsatisfactory though it is, noticeably agrees with the detectable orchard marks, it seems quite likely that these may provide a method of discovering originally timbered areas. Occasionally, some other modern condition will be found that agrees with the historical and orchard-mark data. For example, the long shallow S curve of the present Saratoga Road leading from Santa Clara toward an early redwood lumbering area evidently skirted the main part of the Roblar, cutting inside outliers of woodland that stood in the midst of an oak savanna (*fig. 3*). The outer and the inner border of the northern Roblar were traced respectively by the original main San Francisco road and the upper or cutoff road (*camino de la desecha)* partly represented by present-day El Camino (*fig. 3*, the two roads marked **A** and **B)**.

I have found no historical evidence for or against the presence of trees corresponding to the prominent markings shown on the southeast side of the former bed of Los Gatos Creek in the lower righthand corner of the figures. If such evidence does exist, it may or may not show that this large patch once supported woodland. Elsewhere, the most noticeable orchard damage was in the vicinity of known woodland: around present I-280 in between the San Tomas Expressway and the Saratoga Road about half a kilometer inward from the approximately attested edge of the main Roblar; around present-day Hamilton and Campbell Avenues just southeast of Saratoga Road; and, at the top center of the figures, around the intersection of Remington Drive and Mary Avenue in Sunnyvale.

Near the upper right corner of both figures, there is a conspicuous marking in a place where historical sources suggest that there was a clearing bare of trees. This spot, southeast of the present Wolfe Road–Reed Avenue intersection, was the sink of an old natural drain or overflow stream channel, and perhaps the orchard mark represents something, possibly *A. mellea* or another fungus, existing in the soil and related to the resulting conditions. On the other hand, in the neighboring area at the north end of the historically known Roblar there are relatively few other orchard marks, an absence which might be connected with some condition such as the very close-to-the-surface water table that originally existed there (Clark 1924: 24–25; Cooper 1926: 20–22), or, according to the orchardists' belief, with the relatively large number of oaks that were left standing there until a late date.

During the symposium, a question was privately raised as to whether the distribution of fungus disease might not have been due to heavier irrigation of the fruit trees in some spots, thus stimulating spores widely latent in the soil. If that had been the case, then presumably the reason for overwatering orchard trees would have

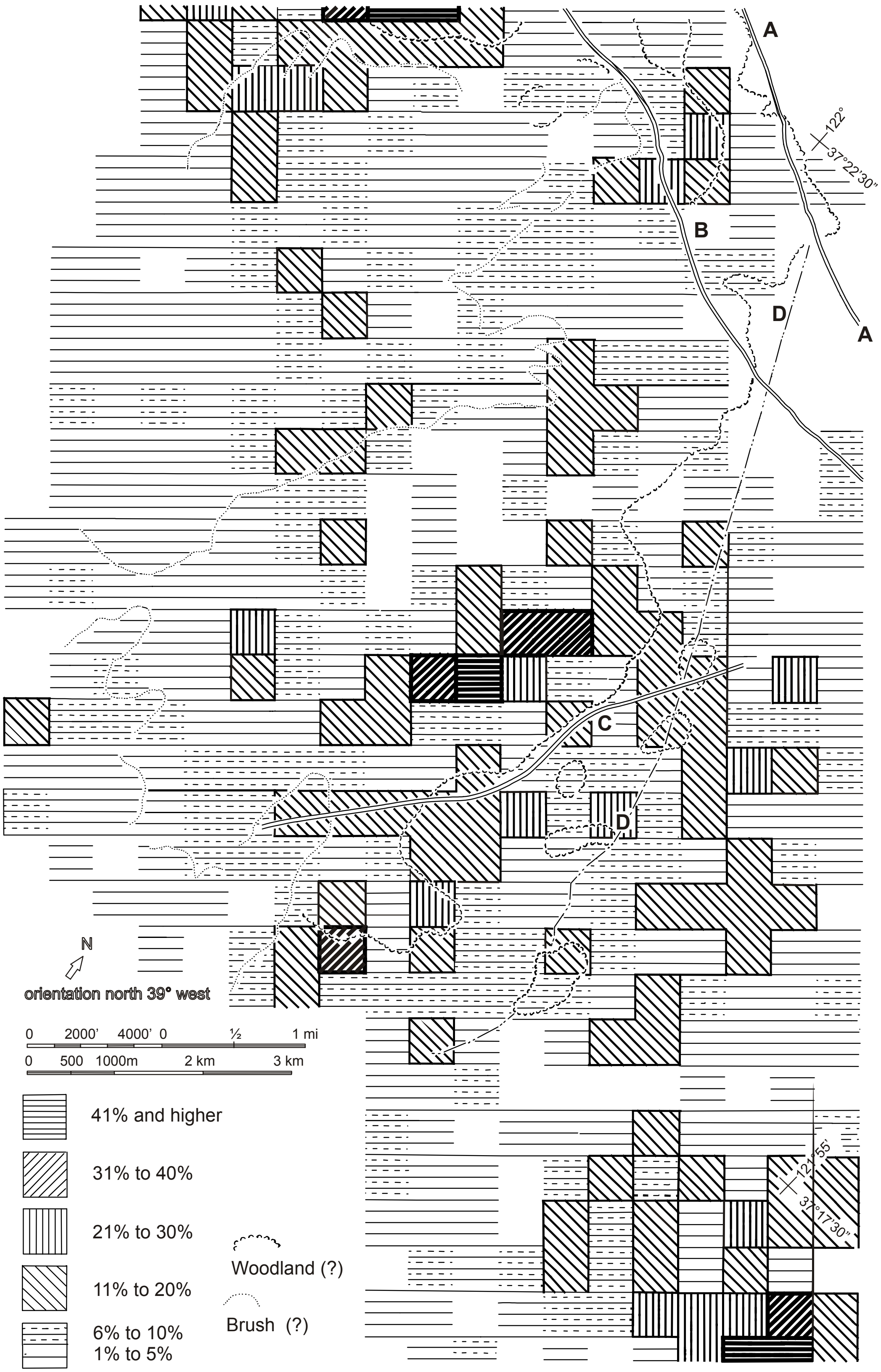

Figure 3—The data of Fig. 2 interpreted as ranges of percentage of visible orchard damage within 25-ha blocks. Scale 1:71,770 at page size.

been the nature of the ground—its water-retaining and runoff characteristics. The four soil classifications that supported the most extensive oak woodland are the same as those that show numbers of orchard marks.[4] These soil types are the Garretson, Pleasanton, Yolo and Zamora series (U. S. Soil Conservation Service c1969: 124, 193–196; cf. Lindsey 1974: 18, 29, 37–38, 63, 65, 67, 71, 75, 77; Welch, Lawrence 1977: 25, 54, 94–95, 107). The soil having the highest proportion (15 percent) of its area in orchard marks is the Garretson gravelly loam, which occurs in fingers of alluvium with a relatively high surface permeability, at the edge of larger old stream-built fans. It is characterized by a somewhat lower available water-holding capacity and a slightly higher runoff rate than surrounding soils. The fairly uniform distribution of fungus-affected patches within this soil type is expressed by the relatively strong correlation (0.63)—as sampled by the individual 25-ha blocks—between the percentages of areas occupied by this soil and areas of affected patches within it. It is possible that orchard trees grown on this soil had to be more heavily watered than others and that the over-irrigation caused the fungus problem to be especially widespread. Alternatively, or additionally, it is possible that the soil itself favored the growth of dense oak woodland—which does happen to be especially well attested for these areas—and that this density was reflected in the later intensity of the oak-root fungus problem.

Of the surrounding soils, a lower percentage (11 percent) of the Yolo loam is within fungus-marked areas, and the correlation (0.36) is much less, corresponding with the historical sources' indications of the uneven distribution of oak woodland, oak savanna, and clearings on this soil type. The Zamora clay loam (7 percent in orchard marks, and 0.30 correlation between these and the soil areas) is not dissimilar to Yolo loam in any of these respects. Yolo silty clay loam likewise has 8 percent of its area in marks and an areal correlation factor of 0.29. The Pleasanton series of soils are very strongly associated with historical attestations of chamisal brush: "unbroken stretch[es] of chaparral with… small islands of live oak and occasional [lone] live oaks scattered through it" (Beardsley in Cooper 1926: 12). These soils are well drained and even rather drouthy, with a very slow surface runoff (U. S. Soil Conservation Service c1969: 165–166; cf. Lindsey 1974: 29, 75; Welch 1975: 22, 80). These qualities would seem likely to increase the necessity of irrigation. However, it is these soils that show the smallest relative percentage of fungus-marked area (6 percent for Pleasanton gravelly loam, 5 percent for Pleasanton loam). Their area correlation figures rank somewhat higher (0.33 and 0.42, respectively), showing the relatively even distribution of marks. In this case, again, the fungus marks seem to have reflected the relative density and distribution of former oak growth rather than any necessary over-watering of orchard trees. On Pleasanton soils near Los Gatos (in the lower lefthand corner of the two figures), no marks appear that could be associated with a large "black oak roblar" mentioned in an early survey (Wallace 1858), where, despite the word *roblar*, "black oak" presumably refers to *Quercus agrifolia* as the dominant species, not *Quercus lobata*. The density of this oak growth is unknown.

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[4] Annotated U.S. Soil Conservation Service aerial photomosaics now held at Loma Prieta Resource Conservation District office, Gilroy, CA; copies supplied by Patricia Marfia, clerk, along with extracts from U.S. Soil Conservation Service c1969.

Conclusion

The present investigation is a qualitative probe. Until any further verification is achieved by comparison with historical sources, or with similar studies for other areas, it must be used only as a hint of where to look for corroborating evidence, historical or other, of oak presence. The approach seems most likely to succeed if applied in such areas as the Santa Clara Valley as a whole and the Brentwood (Contra Costa County) vicinity, and possibly the Clayton and Ygnacio Valleys, all of which had continuous fruit orchard plantings. For areas where there were extensive oak groves but fewer orchards, as in Yolo County, the approach seems less likely to be useful. Quantitative approaches to the problem of locating ancient oak woodlands could, in order to allow further cross-checking between types of data, include in their basis careful attention to oak species, soil types, conditions of culture, former drainage and other topographical elements, and any further information that can be wrung out of existing historical sources. In the mean time, the accompanying diagrams (*figs. 2* and *3*) provide an approximate representation of the belt of mingled valley oak, live oak, sycamore, laurels, and buckeyes that extended for ten or twelve miles around the edge of a large, brush- and live-oak-grown alluvial fan that reached out from the foot of the Santa Cruz mountains. The presence of the main Roblar conditioned early settlement and travel. Its grandeur was appreciated even while economic interests were leading to its piecemeal annihilation. The growers who removed the last trees to make room for their orchards were aware of where the oaks had been, and knew the aftereffects of their existence.

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Age Structure and Growth of California Black Oak (*Quercus kelloggii*) in the Central Sierra Nevada, California[1]

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Abstract

Age structure and growth of California black oak (*Quercus kelloggii*) was determined from tagged trees at four 26.1-acre study stands in Placer County, California. Stands were dominated by large diameter (>20 inch dbh) California black oak and ponderosa pine (*Pinus ponderosa*). Randomly selected trees were tagged in June-August 1998 and harvested under a group selection timber harvest in October-November 1998 and May-June 1999. Trees averaged 148 years of age (range = 58 to 356 years, n = 108), and ages differed among the four stands ($P < 0.006$). Stands had uneven distributions of tree ages, diameters, and heights. A nonlinear regression model was developed that predicted tree age based on diameter ($R^2 = 0.74$). The average 10-year increment of radial growth was 0.72 inches (range = 0.14-2.26 inches, n = 122), and radial growth decreased as basal area increased (nonlinear regression, $R^2 = 0.34$). If average growth rates are desired, basal area retention should average around 100-115 ft^2/acre and 200-225 ft^2/acre for California black oak and all trees, respectively, for stands in the central Sierra Nevada with attributes that are similar to our study stands.

Introduction

California black oak (*Quercus kelloggii*) is widely distributed throughout California's montane environments (Bolsinger 1988, Griffin and Critchfield 1972). Occurring in mostly pure stands or mixed with conifers, California black oak is shade intolerant and a vigorous sprouter (McDonald 1969, 1990). Trees regenerate through stump sprouting or acorn germination, and sprouting is the primary method of regeneration (McDonald 1969, 1990). Because of its sprouting ability, California black oak is thought to primarily occur in even-aged stands as fire is the primary mode of stand replacement (McDonald 1969, 1990; McDonald and Tappeiner 1996). Tree cutting (primarily firewood and occasionally sawlogs) is the land use most affecting this species, but California black oak remains mostly underutilized commercially despite its wide distribution and large timber volume (Bolsinger 1988, McDonald and Huber 1995). In places, California black oak appears to be declining

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as older trees die and are not replaced by younger trees because conifers shade them in mixed-conifer stands (McDonald and Tappeiner 1996, personal observations).

Surprisingly little information exists on the dynamics of California black oak. For sprout-origin trees, a diameter growth model exists for trees from even-aged stands that are < 120 years of age, and a height growth model exists for trees < 170 years of age (McDonald 1969). Powers (1972) developed index curves from higher index sites, and McDonald's (1983) model is based on growth of young trees growing in overstocked conditions where trees had not reached their maximum size and height. Volume tables exist for trees < 30 inches in diameter. A non-quantitative model of diameter-age relationships was described by McDonald (1990), and Savage (1994) developed a linear regression model for diameter-age relationships for trees < 140 years of age. These models are not based on radial stem growth of known age trees from stands with mature trees and cannot predict age from a given diameter beyond 160 years of age. Radial growth is known for trees < 160 years of age, but a statistical model for radial growth was not developed (Gemmill 1980). Seedling occurrence has been associated positively with oak canopy cover and reduced solar radiation (Standiford and others 1997).

Single-tree aging and radial growth models from sites with mature trees would help managers because they would likely differ from models developed with younger California black oaks. Mature trees from uneven-aged stands might also yield different aging and growth equations. In addition, no published information exists on ages of California black oak in mature stands.

We undertook this study of California black oak dynamics, including age and growth, to fill these information gaps. Our objectives were to: (1) determine age structure of several California black oak-dominated stands; (2) develop a model to predict tree age from tree attributes such as diameter and height; and (3) develop a single-tree radial growth model based on several sites in the central Sierra Nevada.

Study Area

We conducted this study primarily on four 26.1-ac study stands in southern Placer County, California. Some additional data were collected from adjacent paired 26.1-ac stands at each site (see below). Elevations ranged from 4,040 to 4,360 ft, and the stands were located on the plateaus and upper portions of steep river canyons that characterize the study area. At the four stands, aspects were W, SE, SW, and S, while slopes were 6 percent, 7 percent, 12 percent, and 33 percent. Study stands were located in larger size, homogeneous forest stands with a tree layer dominated by large diameter (>20 inch diameter breast height [dbh]) California black oak and ponderosa pine (*Pinus ponderosa*). Other less dominant tree species included interior live oak (*Q. wislizenii*), Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), sugar pine (*P. lambertiana*), and incense cedar (*Calocedrus decurrens*). Seedling and sapling California black oak and ponderosa pine dominated the subcanopy at one stand, while the other stands had little subcanopy. The shrub layer was generally sparse, and deerbrush (*Ceanothus integerrimus*) and manzanita (*Arctostaphylos* spp.) were the most common shrubs. The herbaceous layer was dominated by a sparse to dense cover of mountain misery (*Chamaebatia foliolosa*).

Methods

Age (ring count) and growth data were collected from 184 California black oak trees that were harvested in October-November 1998 and May-June 1999 at the four stands. The trees were randomly selected from four 1.5-ac harvest units randomly located in each stand. Stem diameter (inches) at 4.5 ft (dbh) and height (ft) were measured from each tree, which was tagged at ground level with a numbered aluminum tag prior to harvesting. Stumps of the tagged trees were relocated after harvesting. Data were collected during September 1999-April 2000. Tree age (years) based on counts of growth rings was determined from cross-sectional rounds or quarter rounds cut from stumps. Two observers conducted independent counts of growth rings, and their counts were averaged to determine tree age. Average difference in ring counts between observers was 3.8 years (SE = 0.3 years, n = 108) (paired t-test, t = -1.26, df = 107, P = 0.212). Radial growth (inches) for the most recent 10 years (Kertis and others 1993) was determined by measuring the radial distance for the most recent 10 growth rings measured from the outside edge of the cambium into the pith. Two measurements were taken approximately 90° apart, and averaged to estimate radial growth for each tree.

Vegetation characteristics were sampled from 12 0.01-ac plots per stand. Plots were centered on grid intersection points (see below) closest to each tagged tree used for the age and growth models, and three plots were sampled from each 1.5-ac harvest unit. One plot was located at the center of the harvest unit, and the remaining two plots were located on the same or adjacent transect within 82-90 ft of the center plot. Vegetation characteristics measured in each plot were diameter distribution, tree heights, overstory canopy cover, and density (number/ac) and basal area (ft^2/ac) of all live stems > 5 inches dbh.

Timber harvests were conducted on four 1.5-ac circular plots randomly selected from the 15 0.1-ac circular plots in the 26.1-ac stand randomly selected for harvesting. All trees of merchantable size (approximately 8 inches dbh for conifers and 10 inches dbh for hardwoods) were harvested within each 1.5-ac circular harvest unit using a group selection harvest strategy (Davis and Johnson 1987). Stands 3 and 4 were harvested in October-November 1998, and Stands 1 and 2 were harvested in May-June 1999. The staggered harvest was not intentional but resulted from logistic and weather constraints.

Most data did not meet assumptions and distribution requirements for parametric statistics so data were transformed (Zar 1996). Normal probability plots, frequency histograms, and calculations of skewness and kurtosis were used to assess normality of tree and vegetation data, and transformations were selected for each data set that resulted in maximum improvement in each data. Transformations improved normality and equalized variances. Logrithmic10 transformations ($\log_{10} + 1$) were used with tree age, diameter, and heights; crown radius; basal areas; stem densities; and tree diameters and heights from the 12 circular plots. Square root transformations (square root + 0.5) were given to radial growth measurements from individual trees and averages for radial growth of each plot. Canopy cover for all trees, hardwoods, and conifers were given arcsine transformations [arcsine radian degrees (square root (proportion canopy cover + 1))]. Untransformed data were analyzed with some of the nonlinear regressions when the resulting model performed better than models using transformed data or the regression equation used logarithms. Model performance was evaluated based on residual plots and statistical significance of the regressions.

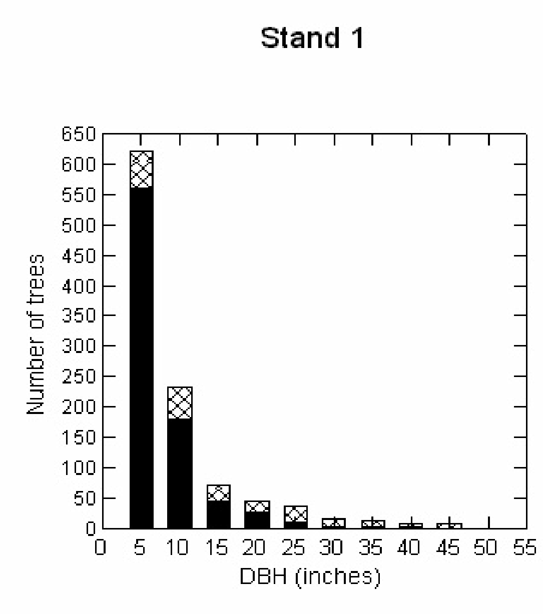
Radial growth was modeled using a distance independent model approach where distances among adjacent trees are not included in the model (Davis and Johnson 1987). Nonlinear regression was used to develop predictive relationships between radial growth and tree age with various attributes of individual trees using a. Simple linear correlation analysis was used to determine initial relationships between vegetation attributes and tree and plot radial growth and age. The variable with the greatest *r* value from the simple linear correlation analysis was used in nonlinear regressions. T-tests were used to determine differences between (1) diameter, height, and crown radius of aged trees and trees that were not aged; and (2) radial growth of trees with and without heartrot. Analysis of variance (ANOVA) was used to determine differences between stands, and Bonferroni pairwise comparisons were used to determine differences between pairs of stands. Kolmogorov-Smirnov two-sample tests were used to determine differences in distributions of ages, diameters, and heights of trees between pairs of stands. P-values were adjusted for multiple comparisons. Statistical analyses were conducted using SYSTAT (SPSS Incorporated 1999a, 1999b).

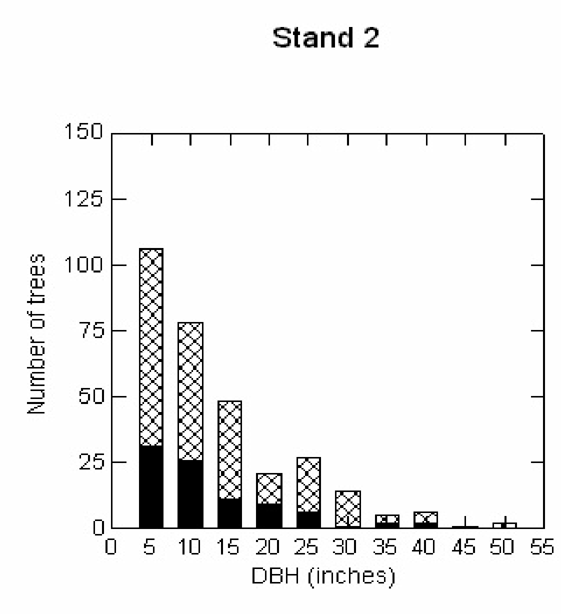
Data were pseudo replicated (Hurlbert 1984) for analysis because tagged trees and vegetation plots from the four stands were treated as replicates in linear and nonlinear regressions and general linear models to increase number of replicates. The four stands are true replicates, but relationships between age and growth with vegetation attributes could not be elucidated with only four replicates. For most regression analyses, summary statistics and scatterplots for each stand are presented to assist interpretation of regression results. Our results and discussion should be cautiously interpreted because of the pseudo replication.

Results

Stand Attributes

The four stands consisted of relatively large diameter California black oaks (dbh average = 18.7 inches ± 1.0 inch SE, n = 4) and smaller diameter conifers (dbh average = 14.3 inches ± 2.3 inches SE, n = 4). Average diameter of all trees was 16.1 inches ± 1.0 inches SE (n = 4). Average tree height of California black oak was 62 ft ± 3 ft SE (n = 4), while average tree height of conifers was 64 ft ± 14 ft SE (n = 4). The stands had large amounts of basal area (average = 200 ft^2/acre ± 21 ft^2/acre SE, n = 4), moderate stem densities (average = 126 trees/acre ± 13 trees/acre SE, n = 4), and closed canopies (average = 61.8 percent ± 3.5 percent SE, n = 4). Basal area of California black oak and conifers averaged 115.5 ft^2/acre ± 11.2 ft^2/acre SE (n = 4) and 84.7 ft^2/acre ± 21.7 ft^2/acre (n = 4), respectively. Stem densities of California black oak and conifers averaged 60 trees/acre ± 11 trees/acre SE (n = 4) and 66 trees/acre ± 11 trees/acre SE (n = 4), respectively. Most vegetation attributes were equivalent among the four stands (F < 2.21; df = 3-4, 10-44; P > 0.100), except stem densities of California black oak (F = 3.11; df = 3, 43; P = 0.036) and conifer stem diameters (F = 2.97; df = 3, 36; P = 0.044). Stand 1 had a more even distribution of diameter classes for hardwoods than Stand 4 (Kolmogorov-Smirnov two-sample test, P = 0.007), while Stands 2 and 3 and Stands 3 and 4 had different diameter distributions of hardwoods (Kolmogorov-Smirnov two-sample test, P < 0.034) (*fig. 1)*.

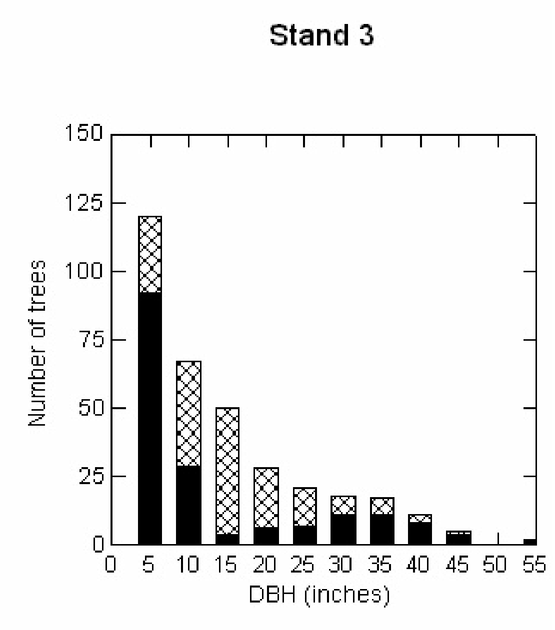




(Figure 1 continued on next page)

Figure 1—Frequency distributions of 5-in diameter (DBH) classes for trees $\geq$ 5 in DBH from four 26.1-ac stands in Placer County, California. Individual bars represent total number of conifer and hardwood trees while pattered portions are for conifers (solid portion) and hardwoods (cross hatched portion) separately.

(Figure 1 continued)



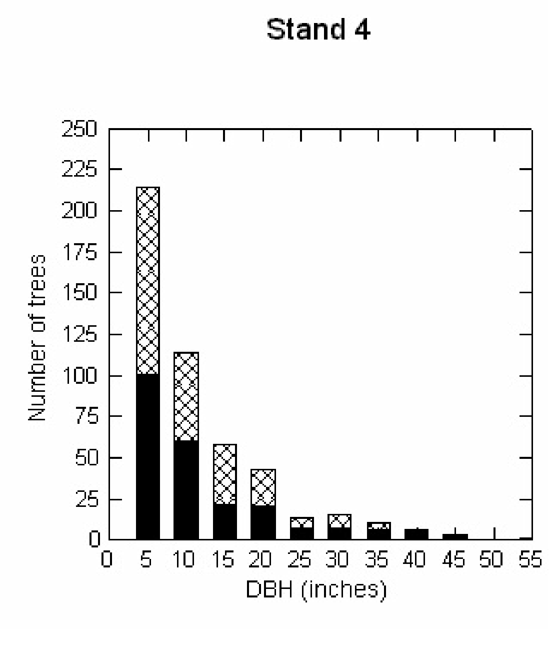


Figure 1—Frequency distributions of 5-in diameter (DBH) classes for trees ≥ 5 in DBH from four 26.1-ac stands in Placer County, California. Individual bars represent total number of conifer and hardwood trees while pattered portions are for conifers (solid portion) and hardwoods (cross hatched portion) separately.

Age

Stand Comparisons

In all stands, harvested trees averaged 147.4 years ± 6.9 years SE old (n = 108) and ranged from 58 to 356 years old (*table 1, fig. 2*). Ages were different among Stands 1, 2, and 4 (F = 5.46; df = 2, 95; P = 0.006) (*table 1, fig. 2*) (Stand 3 was not included because of its small sample size). Trees were older in Stand 1 than Stand 2 (Bonferroni pairwise comparison P = 0.009), while trees in Stand 2 were younger than Stand 4 (Bonferroni pairwise comparison P = 0.049) (*table 1, fig. 2*). Trees were equivalent in age between Stands 1 and 4 (Bonferroni pairwise comparison P = 1.000). There were no differences in diameters of trees that were aged versus not aged for all stands combined (t = 0.067, df = 178.9, P = 0.947) or separately for each stand (t = -0.926 to 0.875, df = 11.1-38.4, P > 0.361).

The four stands had uneven age structures (*fig. 2*). Stands 2 and 4 had a skewed distribution with many trees < 200 years old, and a few trees > 200 years old. Stands 1 and 3 had an equal distribution of trees among age classes *(fig. 2)*. A group of similarly aged trees occurred in Stand 2 where 35 percent (n = 14) of the aged trees were 71-75 years of age. Distributions differed between Stands 1 and 2 (Kolmogorov-Smirnov test, P = 0.009) and Stands 2 and 4 (Kolmogorov-Smirnov test, P = 0.001) (pairwise comparisons did not include Stand 3).

Table 1—*Attributes of harvested California black oaks from four 26.1-acre stands in Placer County, California.*

Attribute	Stand	Mean	SE	SD	Minimum	Maximum
Age (yr)	1 (29)[1]	175.7	17.1	92.1	64	356
	2 (40)	122.7	9.9	62.4	58	315
	3 (10)	145.7	16.9	53.4	68	203
	4 (29)	153.8	10.5	56.4	80	305
	All (108)	147.4	6.9	71.9	58	356
Diameter (in)	1	21.9	2.0	10.6	9.8	46.9
	2	17.5	1.6	10.1	5.9	51.2
	3	19.0	2.5	8.0	8.0	30.7
	4	18.2	1.4	7.7	8.2	38.4
	All	19.0	0.9	9.6	5.9	51.2
Height (ft)	1	75.9	5.8	31.2	20	131
	2	62.7	3.4	21.3	15	104
	3	65.1	7.0	22.2	25	102
	4	56.1	3.0	16.0	20	85
	All	64.7	2.3	24.2	15	131
Crown radius (ft)	1	15.5	1.3	6.9	3.5	33.5
	2	10.4	0.9	5.8	1.0	26.0
	3	12.1	1.2	3.7	6.5	18.0
	4	11.6	1.1	5.7	4.0	29.0
	All	12.3	0.6	6.2	1.0	33.5

[1] Sample size for each stand and all attributes.

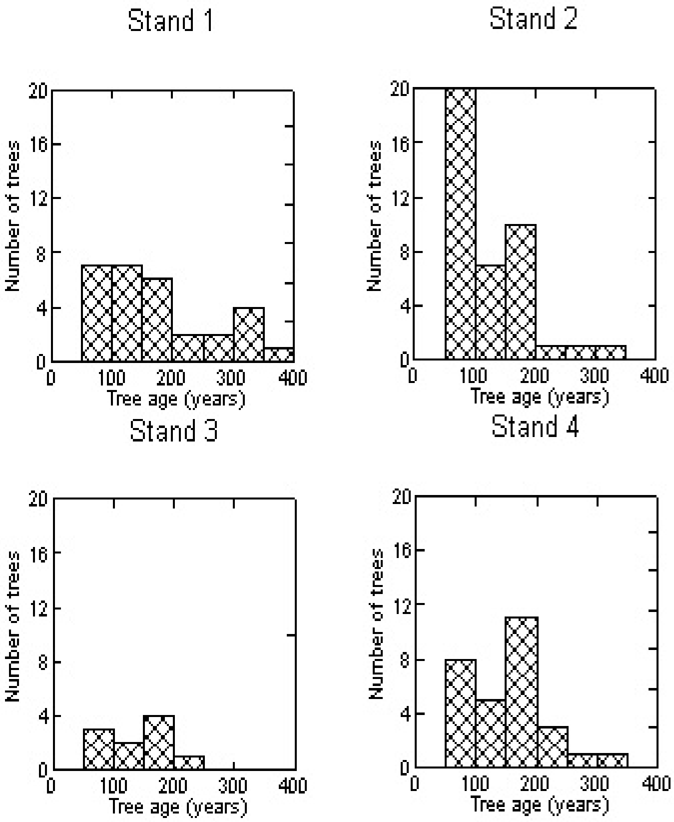


Figure 2—Age class distribution of harvested California black oak *(Quercus kelloggii)* (n = 10-40) from four 26.1-ac stands in Placer County, California.

Aging Model

Average tree age from the 0.1-plots (n = 42-46) was positively correlated with basal area ($r = 0.393$, $P < 0.01$), average dbh ($r = 0.449$, $P < 0.01$), and average height ($r = 0.321$, $P < 0.05$) of all trees. Average tree age was also positively correlated with basal area ($r = 0.572$, $P < 0.001$), average dbh ($r = 0.791$, $P < 0.001$), and average height ($r = 0.427$, $P < 0.05$) of all California black oak in the 0.1-acre plots (n = 41-46). Age was not associated with any conifer attributes ($P > 0.1$).

Tree age was significantly related to tree diameter, height, and crown radius (*table 2, fig. 3*). The best fitting nonlinear model ($R^2 = 0.74$) included a quadratic term for diameter. A similar model ($R^2 = 0.74$) was developed with diameter as the independent variable and tree age as the dependent variable (*table 2, fig. 3*). Models had poorer fits ($R^2 = 0.15$-0.29) for those developed for other tree attributes with age as independent and dependent variables indicating that factors other than age affect these attributes or there is wide variation in the data. We believe that differences in model fit were largely due to variances with the dependent variables. The age-relationship regression lines had a tighter fit along the tree diameter gradient and a poorer fit along gradients of tree height and crown radius (*fig. 3*). In particular, tree heights and crown radii varied widely for trees > 200 years of age.

Table 2—*Best fitting nonlinear regression models for various attributes of California black oaks from four 26.1-ac stands in Placer County, California.*

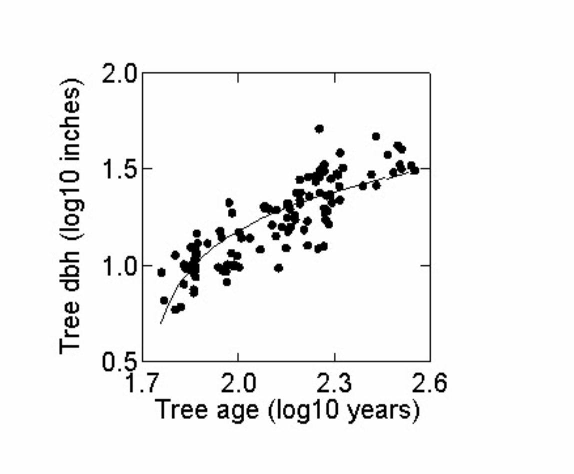
Attribute	Equation	r^2	df	Mean squares Regression	Residual
Age as independent variable					
Diameter[1]	$-1.69 + 1.85*(\text{age}) - 0.22*(\text{age})^2$	0.74	3,105	55.35	0.01
Height	$21.67 + 0.43*(\text{age}) - 0.01*(\text{age})^2$	0.26	3,105	155,884.07	440.50
Crown radius	$-21.83 + 16.08*\log_{10}(\text{age} + 1)$	0.29	2,106	8,711.54	27.79
Radial growth	$2.41 - 0.78*\log_{10}(\text{age} + 1)$	0.15	2,104	30.77	0.15
Age as dependent variable					
Diameter[1]	$-1.06 + 0.92*(\text{dbh}) - 0.04*(\text{dbh})^2$	0.74	3,105	162.90	0.01
Height	$1.20 + 0.52*\log_{10}(\text{height})$	0.21	2,106	243.15	0.03
Crown radius	$1.68 + 0.43*\log_{10}(\text{radius})$	0.28	2,106	234.30	0.03

[1] Log10 transformations to independent and dependent variables.

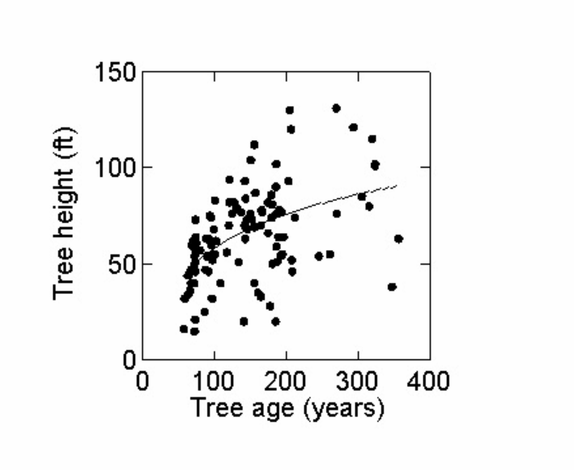
Growth

Ten-year radial growth for individual trees averaged 0.72 inches ± 0.04 inches SE (range 0.14-2.26 inches; n = 122). Growth differed among stands (F = 3.77; df = 3,118; P = 0.013), and Stand 4 had less growth (average = 0.54 inches ± 0.05 inches SE, range = 0.15-1.16 inches, n = 32) than Stand 2 (average = 0.86 inches ± 0.08 inches SE, range = 0.14-2.26 inches, n = 40) (Bonferroni comparison, P = 0.007). Growth in Stand 1 averaged 0.70 inches ± 0.07 inches SE (range = 0.19-1.40 inches, n = 29), while growth in Stand 3 averaged 0.75 inches ± 0.10 inches SE (range = 0.19-2.07 inches, n = 21). Growth averaged 0.72 inches (range 0.19-1.62, n = 46) when calculated on a 0.1-acre plot basis within each stand indicating that plot measures were similar to individual tree measures. Growth within the 0.1-acre plots, however, was equivalent among stands (F = 2.42; df = 3,42; P = 0.079) indicating that it was less sensitive to stand differences; smaller sample sizes with plot data may also have contributed to less discrimination among stands.

A poor fitting model was developed for radial growth and age ($r^2 = 0.15$) (*table 2, fig. 3*). There was considerable variation in radial growth for trees < 100 years of age and less variation for trees > 200 years of age (*fig. 3*). Radial growth from plots was inversely correlated ($P < 0.01$) with basal area of all trees ($r = -0.568$) and conifers ($r = -0.457$) and average diameter of all trees ($r = -0.398$) and conifers ($r = -0.435$) (*fig. 4*). A single outlying datum of low basal area and slow growth reduced the correlation coefficient. Radial growth was variously affected by basal area within each stand (r = -0.182- -0.766, n = 11-12, P = 0.004-0.572) but growth consistently declined as basal area increased. This inverse relationship was stronger for two of the four stands than for data from all stands combined (*fig. 4*).



A.

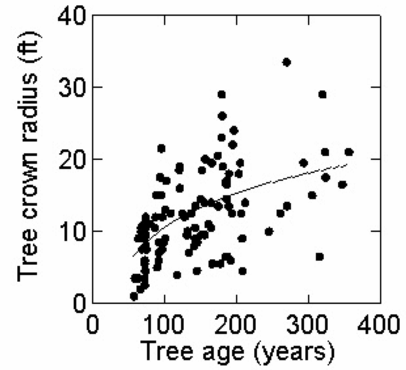


B.

(Figure 3 continued on next page)

Figure 3—Best fitting nonlinear regression relationships between age and (A) diameter, (B) height, (C) crown radius, and (D) radial growth of California black oak (*Quercus kelloggii*) at four 26.1-ac stands (n = 108), Placer County, California. See *Table 3* for regression equations.

(Figure 3 continued)



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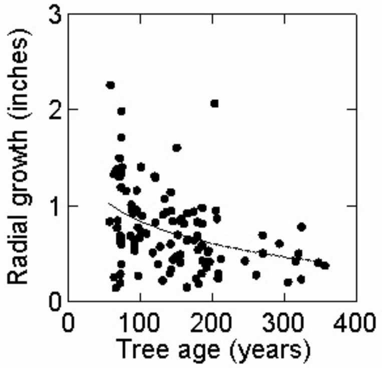

D.

Figure 3—Best fitting nonlinear regression relationships between age and (A) diameter, (B) height, (C) crown radius, and (D) radial growth of California black oak (*Quercus kelloggii*) at four 26.1-ac stands (n = 108), Placer County, California. See *Table 3* for regression equations.

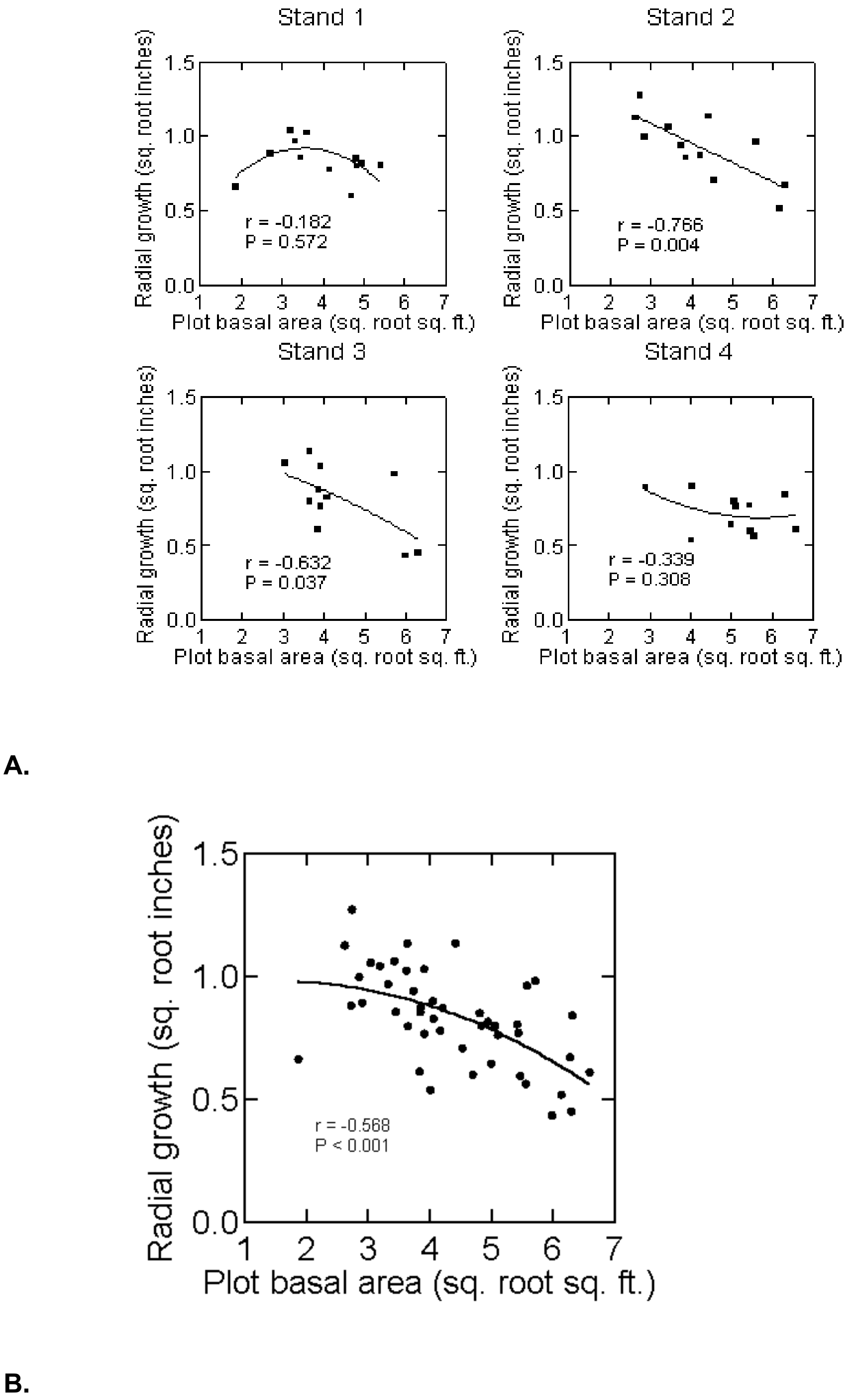

Figure 4—Scatterplots of radial growth of California black oak (*Quercus kelloggii*) and plot basal area from (A) each 26.1-ac stand (n = 11-12) and (B) all stands combined (n = 46) for 0.1-ac plots with > 1 tree measured for radial growth. Lines represent quadratic smoothing and values are correlation results.

Discussion

Stand Attributes

Stands were similar in all vegetation attributes except stem densities of California black oak and diameters of conifers. Our study stands were typical of those dominated by larger diameter and older California black oaks in the central Sierra Nevada, although few stands like this occur in the area. Study stands were selected from over 20 different stands dominated by mature California black oak based on accessibility, high wildlife habitat values, and operability for timber harvesting. California black oak is relatively widespread throughout the study area but occurs in many different stand conditions. Many forestlands in the area, including private and public, have younger trees due to timber harvesting or fire. These age and growth results should apply to most stands with a mixture of California black oak and ponderosa pine that have similar stand attributes.

Age

Trees ranged in age from 58 to 356 years, and there was considerable age variation within each stand. Age distributions were consistent with those of uneven-aged stands (Davis and Johnson 1987). California black oaks generally grow in even-aged stands because trees are replaced by stump sprouting after stand disturbances such as fire and logging top kill trees (McDonald 1978), but uneven-aged trees do occur (Savage 1994). Most previous research on aging, however, has been done on stands with younger trees (< 160 years) and earlier successional stages (Gemmill 1980, McDonald 1978, Savage 1994).

We observed two stand regeneration patterns. The flat age class distribution of Stand 1 indicates regeneration that is sporadic but continuous. Stands 2 and 4 had skewed and bell-shaped distributions, respectively, suggesting that regeneration occurred in pulses. The large number of trees 70-75 years old in Stand 2 indicates a regeneration pulse.

The strong predictive relationship between age and diameter ($r^2 = 0.74$) means that managers have a simple model that can be used to estimate tree age based on diameter. Using these relationships, however, to estimate age structure of a stand of trees should be cautiously done because they produce estimates of age structure that are considerably more continuous than the actual age structure which can be discontinuous (McClaran and Bartolome 1990). The linear regression model developed by Savage (1994) for California black oak had an $r^2 = 0.54$. Poorer fitting models for radial growth, crown radius, and tree height indicate that these attributes are influenced by factors other than age.

Growth

Radial growth over the last 10 years averaged 0.72 inches (range = 0.14-2.26 inches), and variation in growth was greatest with trees < 150 years of age. Radial growth varied within and among stands, and site and stand attributes affected growth. Radial growth over a 60 year period for < 160-year old California black oaks in the San Bernardino Mountains ranged between 0.1-1.1 inches (Gemmill 1980) which was considerably less than radial growth rates from our study. Growth was inversely related to basal area such that growth declined as basal area increased. Average growth occurred at approximately 200 ft^2/acre of which California black oak represented 55-60 percent of the basal area. Growth similarly declines as the number of stems per trees increases (Gemmill 1980). Radial growth of California black oaks from our study in the central Sierra Nevada as well as those in the San Bernardino Mountains (Gemmill 1980) declines as the trees get older.

Acknowledgments

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Coast Live Oak Long-term Thinning Study—Twelve-year Results[1]

Norman H. Pillsbury,[2] Lawrence E. Bonner,[3] and Richard P. Thompson[2]

Abstract

A long-term thinning study was established in 10 stands of coast live oak (*Quercus agrifolia* Née) in the Central Coast of California. Information about diameter, basal area, and volume growth and yield has been obtained from unthinned control plots and from plots thinned to 50 and 100 square feet of basal area per acre measured in 1984, 1989 and 1996. Both basal area and total volume growth percentages were significantly greater in the thinned plots compared to the control plots.

Introduction

This paper is the third report that has been published on this long-term thinning study. The first report described the methodology and rationale for the thinning regime in significant detail (Pillsbury and others 1987).

The second report provided the first information on coast live oak about diameter, basal area, and volume growth and yield from unthinned control plots and from plots thinned to 50 and 100 square feet of basal area per acre measured. These results were reported in the proceedings of the 1990 oak symposium (Pillsbury and Joseph 1991).

This, the third report, extends our knowledge about the effects of thinning in coast live oak stands to a 12-year period.

There are no past or current studies that show the effects of thinning on the growth of coast live oak residual stands. Thinnings are normally conducted to stimulate the growth of the trees that remain and to increase the total yield of useful fiber from the stand. The basic objectives of thinning are: a) to redistribute the growth potential of the stand into fewer but larger trees, and b) to utilize all the merchantable material produced by the stand prior to harvest (Smith 1962).

The age that the final harvest would occur (rotation) for coast live oak was examined in a preliminary site, growth and yield study on the Central Coast (Pillsbury and De Lasaux 1985). Based on the growth rate and stand condition, a

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[1] An abbreviated version of this paper was presented at the Fifth Symposium on Oak Woodlands: Oaks in California's Changing Landscape, October 22-25, 2001, San Diego, California.

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biological rotation of a stand could be as early as 50 years, although a harvest at age 75 or 80 would be feasible especially for stands on lower quality sites.

Currently, little is known about site productivity, regeneration, tree growth and the potential effects of harvesting on oak woodlands. Little information is available on different management practices and their effects. By developing a number of permanent plots, growth can be documented over time. These data will prove valuable to foresters and landowners that wish to maximize fiber production in existing stands or want to compare the potential for different management strategies.

The primary long-term goal of this study is to establish a series of permanent plots to develop long-term diameter, basal area and volume growth and yield information for thinned and unthinned stands of coast live oak in Monterey, San Luis Obispo, and Santa Clara counties.

Many of the stands measured in previous studies are near rotation age, therefore it is important to know if they could benefit from thinning. This study may help to determine if thinning of older stands will yield increased fiber while allowing for immediate income from the removed trees.

Methods

Site and Plot Selection

Ten sites were selected for this study and were distributed as follows: Monterey County—four sites; San Luis Obispo County—five sites; and Santa Clara County—one site *(fig. 1, table 1)*. Three plots were established at each site consisting of one control plot and two plots that were thinned to 50 and 100 square feet per acre, respectively. Plots were established in stands approximately 40 to 85 years old.

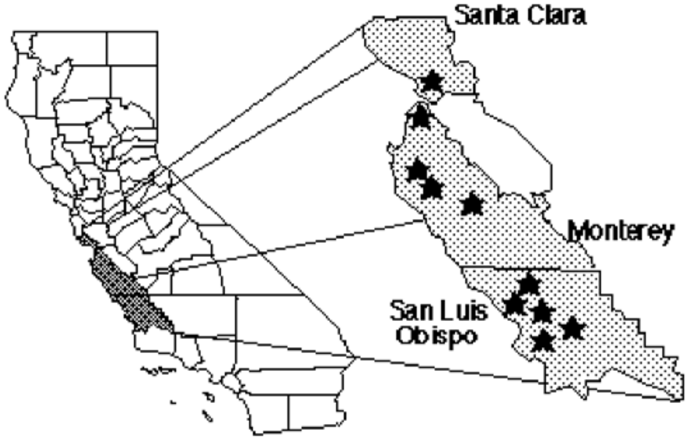

Figure 1—Map of coast live oak thinning plots.

Each plot is one-fifth acre in size and surrounded by a two-fifths acre buffer zone for a total area of three-fifths acre. Plots were established by compass and tape; metal rebar was used to monument plot corners.

Table 1—*Location, treatment and plot description.*[1]

	Treatment by site and plot number		
Location/USGS Quad./County	**Control**	**100 sf/ac**	**50 sf/ac**
Cuesta Grade/Lopez Mountain/San Luis Obispo	1-2	1-1	1-3
Elkhorn Slough Estuarine/Prunedale/Monterey	2-2	2-3	2-1
Arian Ramage/Adelaida/San Luis Obispo	3-3	3-2	3-1
San Carlos Ranch/Mt. Carmel/Monterey	4-3	4-1	4-2
Chualar/Gonzales/Monterey	5-2	5-3	5-1
Castro Valley Ranch/Watsonville/San Benito	6-2	6-3	6-1
Rana Creek Ranch/Rana Creek/Monterey	7-3	7-1	7-2
Presenti Winery/Templeton/San Luis Obispo	8-3	8-1	8-2
Prefumo Cyn/Morro Bay South/San Luis Obispo	9-3	9-1	9-2
Lopez Lake/Lopez/San Luis Obispo	10-2	10-3	10-1

[1] 1-2 means Site 1, Plot 2.

Data Collection

The following information was obtained for each tree in 1984, 1989, and 1997 (and was re-measured in summer 2001): tree number, species, dbh (inches), total height (feet), tree vigor (code) and crown class (code). The same data was collected for trees in the control plot.

The following plot information was obtained for each plot in 1984, 1989, 1997 (and was re-measured in summer 2001): percent crown closure, percent ground cover (bare ground/rock, grasses and forbs, and litter), percent and species of woody shrub cover, forage (species, extent and weight), sprouts and stumps (clump diameter, sprout height, sprout number, stump diameter, stump height, stump angle) and surface erosion (type and percent). Additional tree information obtained during the initial inventory in 1984 includes the following: merchantability indicator (code), azimuth from plot center and distance from plot center. The original azimuth and distance information is used in each analysis to plot planimetric stem maps.

Additional plot information obtained during the initial inventory in 1984 includes the following: slope (percent), aspect, elevation, soil type, site age and site index. Plots were identified by quad name, taken from USGS 7.5 ft topographic maps, by aerial photographs, planimetric stem maps (showing tree location and its relative size) and by plot access information consisting of a detailed plot location narrative, sketch and ownership information for each site.

Development of Stand, Basal Area and Stock Tables

Basic mensurational data were compiled for each plot before and after thinning and extrapolated to a per acre stand basis. A stand table consisting of the number of trees of a given species per diameter class per acre was developed. Trees were grouped into two-inch diameter classes. Basal area tables were also developed by species and diameter class on a per acre basis. Stock tables, the cubic foot volume of trees of a given species per diameter class per acre, were also developed.

Tree volumes for hardwoods were computed according to three utilization standards, total volume, wood volume, and sawlog volume. Total volume is the total outside bark volume including the stump. Wood volume is inside bark volume from stump height (1 foot) to a 4-inch top (inside bark) for all stems. Sawlog volume is the inside bark volume found in trees having an 11-inch or greater dbh and have straight, sound segments 8 feet or greater in length, from stump height to a 9-inch top diameter inside bark (Pillsbury and Kirkley 1984). Only total volumes were computed for non-hardwood species.

Using a computer application (Future Basic II),[4] a series of computer subprograms were written to develop the 90 stand, basal area and stock tables plus a number of other tables needed to summarize the data. From this array of information we were able to begin to chart the course of stand growth and change in the coast live oak thinning plots. Standard mensuration formulae were used to calculate basal area, number of trees per acre and tree volume.

Results of 1996 Re-measurement of Stands

Only the results of the primary long-term goals of the study are presented here. Analysis and results for the following subtopics: wood volume, sawlog volume, tree movement by diameter class, economics, predicting incomes and rates from sustained thinning, economic considerations based on forage, wildlife and aesthetics, and changes in the forage layer in the thinned plots, can be found in Pillsbury and others (1998).

Twelve-year Results of Thinning Treatments

Coast live oak plot data were analyzed for change in stand density and growth volume. The effects of the thinning treatments after twelve years on stand characteristics including number of stems, basal area, and total volume is discussed.

Number of Stems per Acre

In the control plots, a decline in the number of trees per acre is seen primarily due to mortality *(fig. 2)*. The thinned plots saw little change since the initial thinning.

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[4] Mention of trade names or products is for information only and does not imply endorsement by the U.S. Department of Agriculture.

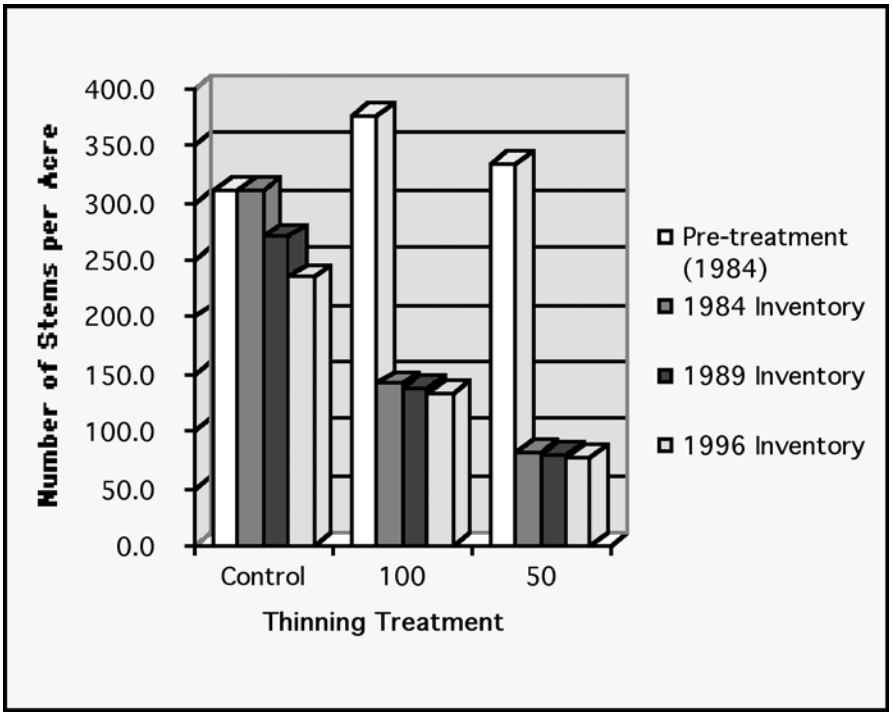


Figure 2—Number of stems per acre by treatment type.

Any change in the number of stems per acre that would occur would be due to either in-growth or mortality. In-growth, when trees finally reach 4.5 feet in height and 1.0 inches in dbh and then would be included in the sample, only resulted in six trees for the 10 sites. On a number of sites it was observed that sprouts were nearly tall enough to be classified as trees and it is expected that the next inventory will show the first substantial ingrowth. Stump sprouting and the growth and development of sprouts are examined in a later section.

Mortality, however, did occur and had a definite impact on the study, especially for the control plots *(fig. 3)*. The wildfires that occurred during the summers of 1985 and 1994 produced very intense conditions and were responsible for the majority of tree death that occurred. A total of three of the 10 control plots were affected by fire between inventory dates of 1984 and 1989 and one control plot between inventory dates of 1989 and 1996. An average of 76 trees per acre was lost during the 12-year interval. The majority of trees lost in the first inventory were in plot 1-2, which lost an average of 215 trees per acre. The 1996 inventory showed a serious loss again in plot 1-2 of 110 more trees per acre. In effect, plot 1-2 lost 325 of its 400 trees per acre from 1984 to 1996 due to fire, or 42 percent of the total lost in all control plots.

During the 1984-1989 period, both fire and snow significantly affected site 3. While only 30 trees/acre that were damaged by one or both of these events died during the first 5-year period, an additional 160 trees per acre died during the next seven years.

By contrast only an average of 31 trees/acre died from other causes in the other eight control plots, and only an average of 8.5 and 4.0 trees per acre died in the 100 and 50-ft^2/acre plots, respectively. The greater density of trees in the unthinned control plots certainly contributed to the fire intensity and subsequent loss. The effect of repeated fire in unthinned stands cannot be ignored.

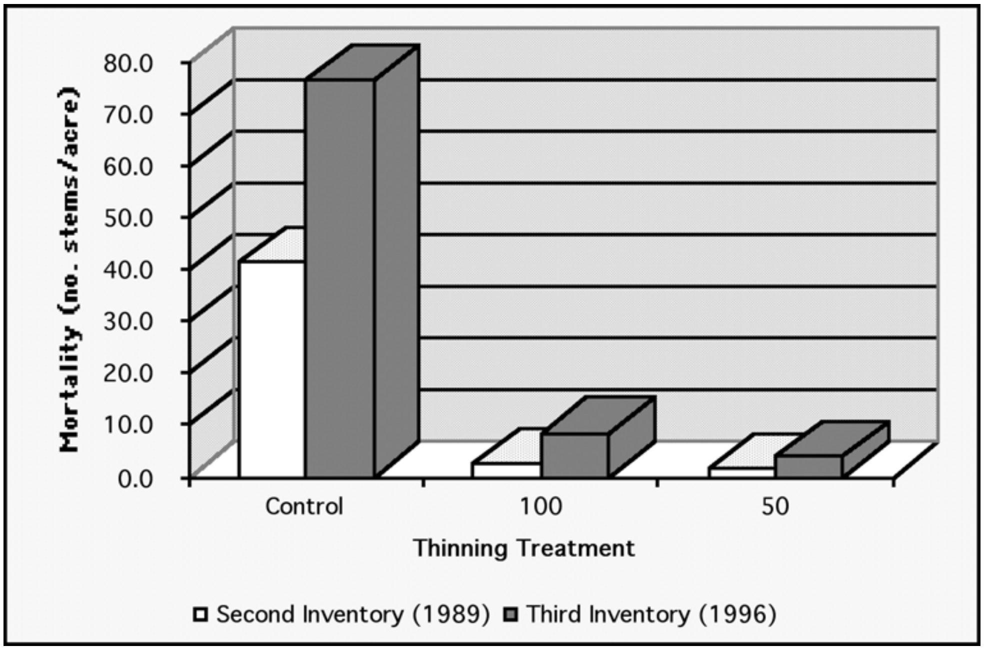
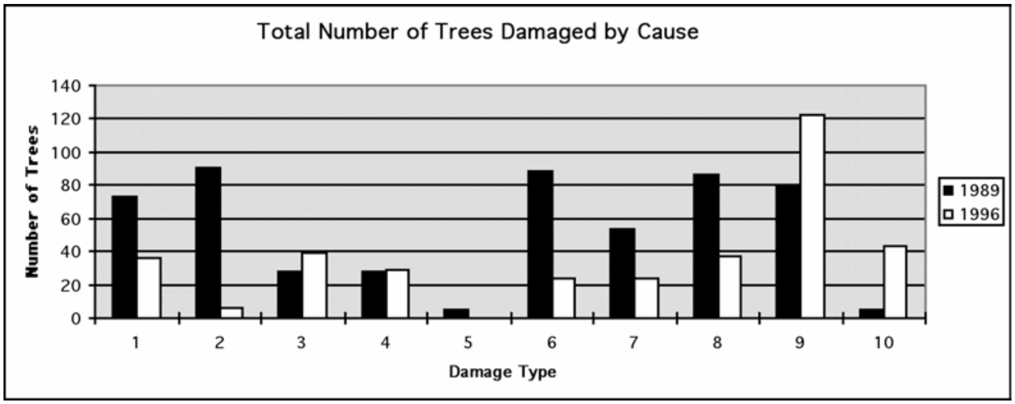


Figure 3—Mortality for control and treatment plots.

In addition to the outright death of trees from fire, a number of factors contributed to tree damage during this period *(fig. 4)*. Again, wildfire played an important role. Many trees had scorched trunks, burned crowns and cracked or swollen bark making diameter measurement difficult. Trees, which were defoliated by the flames often, produced sprouts along the stem and branches. Although they were classified as a living tree, their rate of growth will be greatly reduced.



Code	Damage Type	Code	Damage Type	Code	Damage Type
1	DT=Dead Top	5	SB=Sprouts-basal	8	YD=Fire Damage-effects diameter
2	S=Snow Damage	6	SP=Sprouts-other	9	CB=Cracked Bark
3	BT=Broken Top	7	Y=Fire Damage-no diameter effects	10	BI=Basal Injury
4	SS=Sprouts-stem				

Figure 4—Mortality by damage type. Note the incidence of damage types appears to have decreased. This is because most of the trees that were affected in the 1989 inventory died by the 1996 inventory.

Basal Area Per Acre

Basal area was the variable used to design the thinning treatments in 1984. The changes that occurred in basal area are shown in *figure 5*.

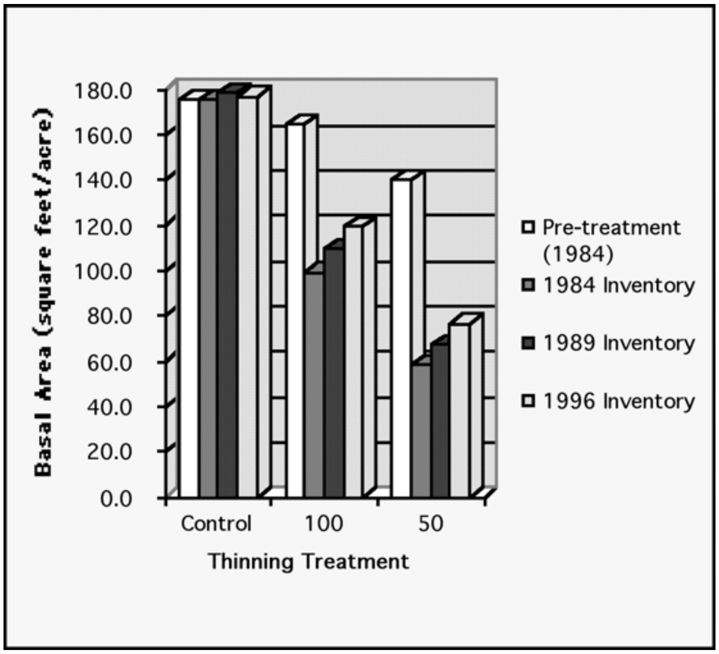


Figure 5—Basal area per acre for control and thinned plots.

The twelve-year average increase for all control plots is 1.5 ft^2/acre or about 0.85 percent for the 5-year period. The more heavily thinned (50 ft^2/acre) plots increased by about 17.9 ft^2/acre (30.5 percent) while the 100-ft^2/acre plots increased by 20.0 ft^2/acre (20.1 percent) during the same period.

Further, these data show that the 50-ft^2/acre plots averaged 21 times the basal area growth when compared to the control plots *(fig. 6)* and the 100-ft^2/acre plots averaged 23 times the growth compared to the control plots.

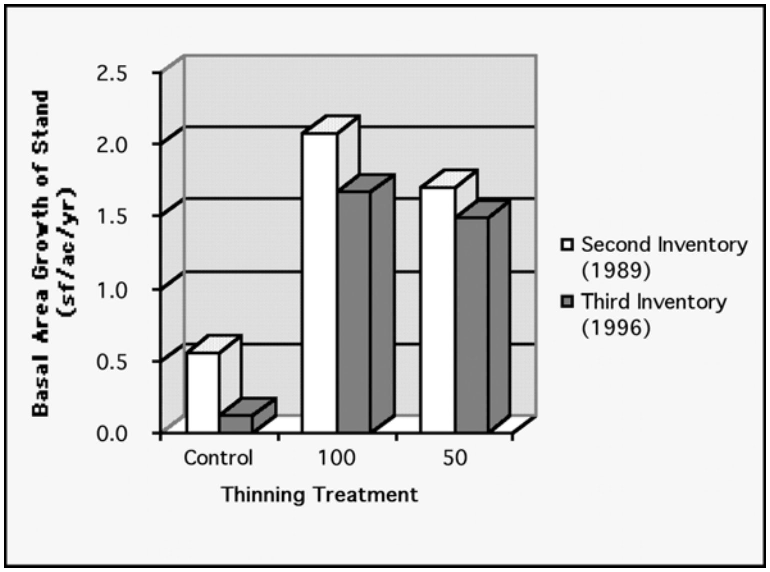


Figure 6—Basal area growth of stand for control and thinned plots.

It could be argued that these ratios and data might be somewhat misleading because of the high rates of mortality in the control plots. On the other hand, one of the reasons for thinning a stand is to reduce the density quickly i.e., speed up the rate of natural mortality, and to improve the vigor and growth rates of the remaining trees. Dense stands will typically have higher rates of natural mortality as well as higher death rates during catastrophic events such as wildfire and extreme snowstorms. In an effort to provide a comparison of how surviving trees responded relative to the control plots, the analysis from this point on is only conducted on living trees.

Because of the mortality caused by fire and snow, these data show not only the positive results of thinning but also the loss of growth that can occur when stands are not properly managed.

Total Volume in Cubic Feet per Acre

During the twelve-year period, total volume increased by 799 ft^3/acre (16.2 percent) for control plots *(fig. 7)*. Thinned plots incremented by 914 ft^3/acre (32.0 percent) for the 100-ft^2/acre plots and by 701 ft^3/acre (40.4 percent) for the 50-ft^2/acre plots.

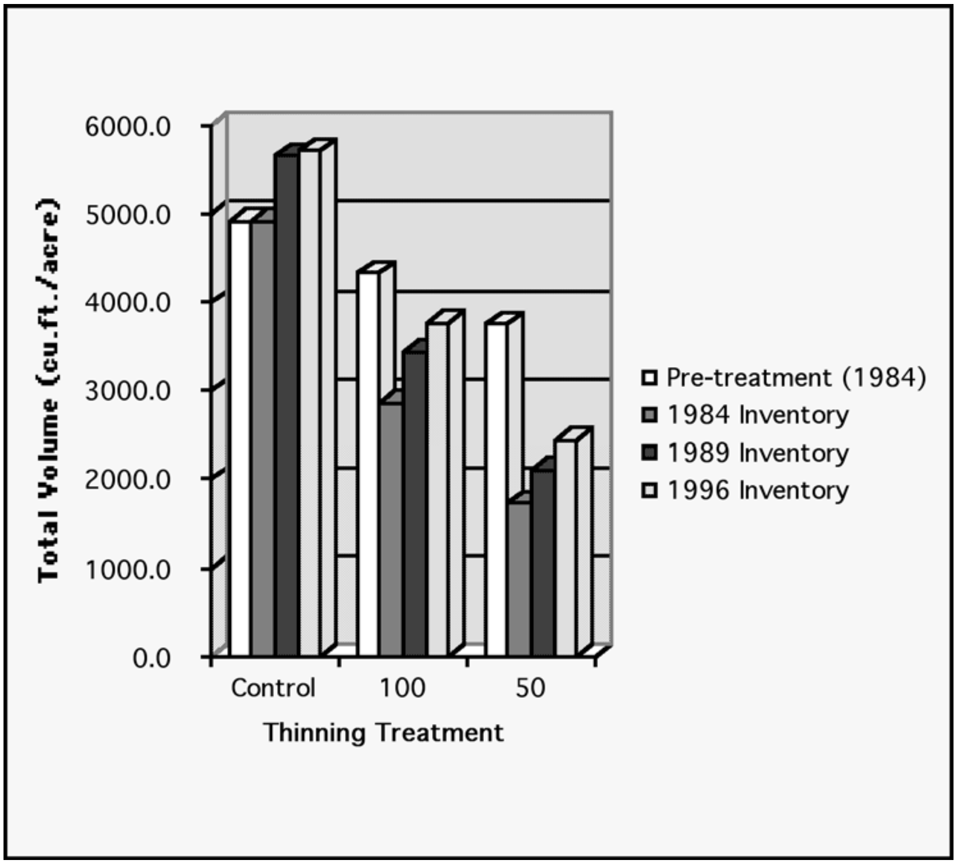


Figure 7—Total volume for control and treatment plots.

Further it must be understood that control plots contain many more trees than the thinned plots and that the total volume growth could be greater simply due to the total number of trees. In total they could produce more volume even though their growth rates might be slower. For this reason, a more realistic comparison of growth is to calculate growth per tree.

The data show that the thinned plots out grew the control plots by substantial margins *(fig. 8)*. The 100 ft^2/acre plots incremented 50 percent more total volume and the 50 ft^2/acre plots incremented 91 percent more total volume than did the control plots.

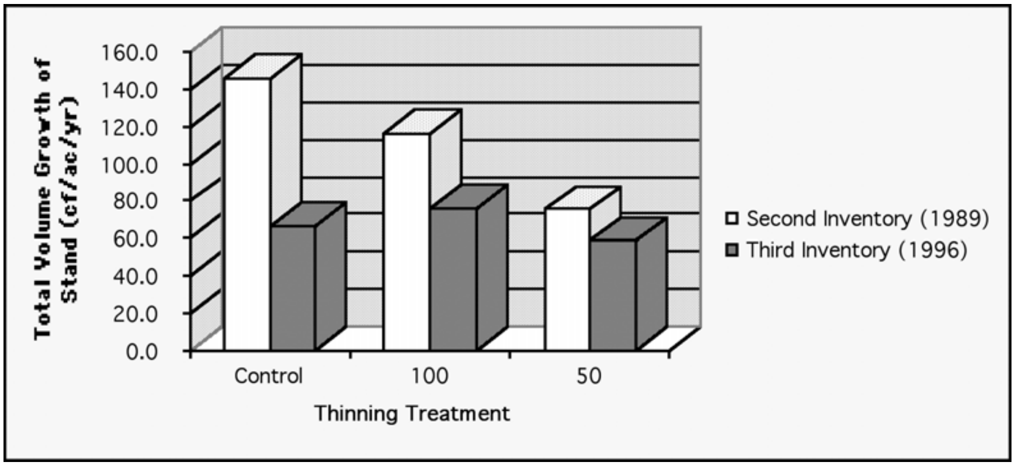


Figure 8—Total volume growth per tree for control and treatment plots.

The U.S. Department of Agriculture-Forest Service (1977) uses the following definition for Productive Forest Land: "Land which is physically capable of producing crops of industrial wood in excess of 20 cubic feet/acre/year." While the wood products from coast live oak are mostly in the form of firewood, it is interesting to note that the rate of growth of coast live oak exceeded 20 cubic feet/acre/year for all plots.

The results of this study were compared with a stem analysis study conducted on 25 plots in 1985 (Pillsbury and De Lasaux) with similar results. All plots in the 1985 study exceeded 20 cubic feet/acre/year based on the mean annual increment (MAI), and all except one exceeded this value for the coast live oak study.

A similar MAI analysis was conducted for this study. It shows that the MAI of control plots has peaked and is now declining while the MAI of the thinned plots is still increasing. Thus the overall productivity of non-thinned plots will likely continue their decline, however, cutting treatments of the thinned plots appears to have prolonged stand productivity.

Analysis of Plot Regeneration

The revegetation of live oaks through the sprouting of cut stumps, otherwise known as coppice management, is widely used in a variety of forestry and woodlot situations. California coast live oak is well known as a vigorous sprouter. This is especially true when damage is created by fire, wind or harvesting. Most common are sprouts from the cambial layer which form a ring on top of the stump.

In this study sprouts took on two distinct forms: 1) mound or "clump" form, and, 2) sprouting form. Clumps occurred when the succulent sprouts were browsed by wildlife and domestic animals. These sprouts become rounded into a dome or mound shape. The mounds continue to expand outward, growing mostly in diameter rather than height, until an animal can no longer reach the sprouts in the center or until a growing season passes when browsing fails to occur. The center sprouts then will “escape” and grow into a new tree. This process could take anywhere from two or three years up to 15 or 20 years. If the stump had one or more dominant leaders it was classified as a sprout (as opposed to a clump).

In order to better understand the process of tree development from clumps, they were grouped into three size categories. For the 100-sf/ac lightly thinned plots, 34 percent of all clumps were less than two ft. in diameter, with 53 percent two ft. to three ft. in diameter, and 13 percent greater than three ft. in diameter.

For the 50-sf/ac heavily thinned plots, 35 percent of all clumps were less than two ft. in diameter, with 41 percent two ft. to three ft. in diameter, and 24 percent greater than three ft. in diameter.

By our definition, a mound ceases to be classified as a mound when at least one sprout attains a height of least three inches and is unbrowsed. Therefore, over time it would be expected that as mounds begin to produce sprouts, the number of mounds surveyed would decrease and the number of stumps that were classified as sprouts would increase.

In the 100-sf/ac plots there was a large decrease in the number of mounds *(fig. 9a)*, however it is not clear that this decrease resulted in a corresponding increase in sprouts *(fig. 9c)*. In the 50-sf/ac plots a closer correlation can be seen as three of the four sprout height classes showed an increase *(fig. 9d)* likely due to the decrease in the number of mounds *(fig. 9b)*.

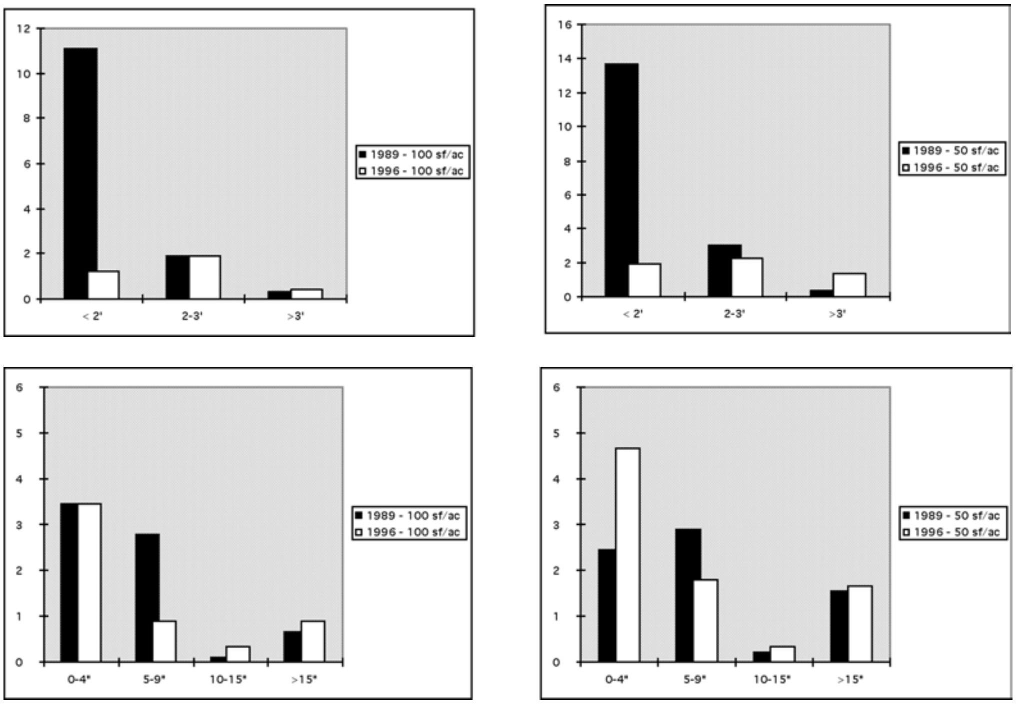


Figure 9—a) Clump data for 100-sf/ac plots. b) Clump data for 50-sf/ac plots. c) Sprout data for 100-sf/ac plots. d) Sprout data for 50-sf/ac plots.

Site 5 was the first to show signs of natural regeneration. The more heavily thinned 50-sf/ac plot (5-1) had 31 natural sprouts ranging from 4-19 inches in height while plot 5-3 had two natural sprouts ranging from 10-12 inches. Natural regeneration will be closely monitored in future inventories.

Conclusions and Recommendations

The first twelve years of growth information has been collected and analyzed for the coast live oak thinning study. The interpretation of this data is discussed below in the form of conclusions and recommendations.

1. Two major forest fires occurred during the 12-year interval, which affected the study. Our data shows that the more dense, unthinned plots sustained greater damage from fire than did the treatment plots. Proper care and management of the woodland forest can reduce losses from fire and, in general, protect the value of the resource.

   Many of the stands in the thinning study are thought to be near rotation age. Could they benefit from a thinning at this age? The answer to this question is "yes." The benefits were already apparent after the 5-year inventory, and that trend has strengthened after twelve years of growth.

2. Both basal area and total volume growth percentages were significantly greater in the thinned plots than the control plots. Average per acre growth rates for the 12-year interval ranged between 20 and 31 percent for treatment plots but only 1 percent for control plots. In general, total volume growth was approximately twice as great in the treated plots compared to control plots. Clearly coast live oak stands, even if they are older, respond in a positive manner to thinning.

3. Prior to thinning, all 30 plots in the study were measured and their growth rates were found to exceed the Forest Service definition for Productive Land (20 ft^3/acre/year). In fact they averaged about 70 ft^3/acre/year. An independent site, growth and yield study conducted on 25 plots in San Luis Obispo and Monterey counties in 1985 showed similar results. In that study, coast live oak plots averaged about 60 ft^3/acre/year. In both studies the researchers sampled only moderately dense to dense stands; the typical growth pattern for coast live oak.

   This information is significant as it relates to the potential for silvicultural practices and management for commercial products.

4. Cut stumps on thinned plots were evaluated for their ability to produce sprouts. Less than one-third of the stumps produced clumps (a dome-shaped mass of stems created by heavy browsing) by the end of the 12-year period, and only about 15 percent of the clumps were able to "escape" into the sprout stage.

   This means that regeneration by coppice methods is not going to occur rapidly following thinning by itself. Some method of protection, such as screens or piling brush on the stump, is necessary to encourage more rapid regeneration.

5. The condition of the soil was evaluated in 1984, 1989 and 1996. No type or amount of erosion was observed on any plot regardless of the land slope. Apparently the crown and root density left after thinning was sufficient to protect the site.

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Plant Diversity and Invasives in Blue Oak Savannas of the Southern Sierra Nevada[1]

Jon E. Keeley[2]

Abstract

Blue oak savannas were found to be substantially more diverse at all scales from localized point diversity to the community scale, than higher elevation shrubland and coniferous forests in the southern Sierra Nevada. Also, alien plants were more diverse and represented a substantial fraction of the understory flora in these blue oak savannas, comprising three-fourths of the species at the smallest scale (1-m^2) and about half at the largest scale (1,000-m^2). Either alien invasion has greatly increased species diversity in these savannas or it has displaced native annuals as opposed to native bunchgrasses as is commonly proposed. Livestock grazing is thought to have played a decisive role in the initial invasion of the blue oak savanna understory. Today there are differences evident between livestock grazed and ungrazed sites and between horse and cattle grazed sites. Grazed sites have slightly higher species richness and higher alien species richness and cover than ungrazed sites. The differences, however, are rather subtle and despite over a century of protection from livestock grazing, ungrazed sites are remarkably similar to sites with a continuing history of grazing.

Introduction

Blue oak (*Quercus douglasii*) woodlands are the most extensive hardwood cover type in California (Bolsinger 1988), often forming open savannas *(fig. 1)* with an understory dominated by annual grasses and forbs. Although these savannas have a rich flora of natives, a substantial portion of the herbaceous understory comprises non-native species (Borchert and others 1993). This alien understory is dominated by annual grasses and forbs endigenous to low elevation habitats in Eurasia (Baker 1989). It is generally assumed that this invasion is an extension of the alien invasion that occurred in native bunchgrass prairies, driven by a combination of livestock grazing and severe drought during the 19th century (Burcham 1957). Alternatively, it has been suggested that these savannas were formerly closed canopy blue oak shrublands that had been opened up by frequent anthropogenic fires (Cooper 1922, Griffin 1977).

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Figure 1—Blue oak savanna in the foothills of the southern Sierra Nevada. (Photo by author).

Disturbances in the form of intensive grazing and fire often favor invasion of natural ecosystems, although natural diversity patterns have long been considered to play a role in providing some level of resistance to invasion (Elton 1958). Thus, both patterns of disturbance and species richness are potential factors affecting community invasibility. Some communities are capable of closer species packing, and thus higher species richness than other communities, presumably making them less susceptible to invasion by alien species. Data both support (Fox and Fox 1986) and refute this prediction (Stohlgren and others 1999) and some of the potential explanations for community differences include differential impacts of various growth forms and different scales over which species richness is examined (Huston 1994). Propagule availability is also a potentially determining factor (D'Antonio 2000). For example, the proximity of alien populations may play a critical role in the invasion process. Thus, broad landscape patterns of alien distribution may be important in understanding the invasion process as concentrations of aliens in one community could influence invasion of adjoining communities.

Of particular concern to resource managers is how to predict which species are likely invaders, which communities are most at risk to invasion, and how land management practices influence the invasion process. In order to gain a picture of these patterns in the southern Sierra Nevada this study was undertaken to evaluate plant diversity and alien distribution across a broad scale from the localized point level to the community level and how they differ across the landscape. Specifically, patterns of species richness and alien plants were evaluated under cattle and horse grazing in blue oak savannas and these patterns were compared with other plant communities in and adjacent to Sequoia and Kings Canyon National Parks.

Study Sites and Methods

This study was conducted in the foothills and mid-elevation range of the southern Sierra Nevada, in or adjacent to Sequoia and Kings Canyon National Parks. All blue oak savanna sites were located within a 10 km radius of the Ash Mountain entrance station to Sequoia National Park, either on National Park land or Bureau of Land Management land. These blue oak savannas were dominated by oaks *(Quercus douglasii)* and buckeye (*Aesculus californicus;* nomenclature according to Hickman 1993). A total of 15 oak savanna sites between 440 and 680 m were sampled during the late spring and early summer of 1999. Sites differed with respect to their livestock grazing history: five had been grazed seasonally by horses, five grazed seasonally by cattle, and five with no livestock grazing since the founding of the national park in the 19th century. Fire history for the oak savanna sites was uncertain but none had burned recently. For comparison with the oak savanna sites, higher elevation chaparral, between 860 and 1,280 m, and mixed coniferous, between 1,400 and 2,400 m, were sampled. These sites had a complex fire history with many having burned in recent years and are described more fully in Keeley and others ([In press]).

Sites were selected from a GIS layer of plant association types and a layer of each of the required treatment conditions. Study sites were selected by picking random numbers for UTM coordinates between 50 and 200 m off a road. If ground truthing revealed sites had unanticipated disturbances, either natural, e.g., landslides, or anthropogenic, these were eliminated and new coordinates selected. Surface litter was collected within a 20-cm diameter hoop from three alternate plots at each site, dried and weighed. Three soil samples from the top 6 cm were collected from alternate plots and combined. Texture analysis was done according to Cox (1985). From a subsample, pH was determined in an equal mixture of soil and dH_2O. Soil nutrients, NO_3, NH_4, P, and K were determined on a subsample at the Soils Laboratory, University of California, Davis.

Vegetation sampling was a modified Whittaker plot (Keeley and others 1995, Schwilk and others 1997); a 0.1 ha (20 x 50 m) site was subdivided into 10 non-overlapping 100-m^2 (10 x 10 m) plots and nested in the outer corner of each plot was a 1-m^2 (1 x 1 m) subplot, which was sampled for density and cover (in chaparral and forested sites with sparser herbaceous vegetation an additional subplot was sampled on the inside corner of each plot). Within the 100-m^2 plot, additional species not in the subplots were recorded. A total of 15 blue oak savanna sites, 10 chaparral sites and 103 coniferous forest sites were sampled. Comparisons between vegetation types were with one-way Analysis of Variance (ANOVA).

Results

Landscape Comparisons

These blue oak savannas were relatively open with generally less than 30 percent canopy coverage. The herbaceous understory was quite diverse and species richness was markedly higher than for chaparral and coniferous forests, at both the point (1-m^2) and community (1,000-m^2) scales *(fig. 2A-2B).* In blue oak savannas alien species comprised nearly three-fourths of the species at the smallest scale and about half at the largest scale *(fig. 2A-2B)*. If alien species were subtracted from the total species richness then blue oak savannas and coniferous forests would be comparable in species richness at both the 1- and 1,000-m^2 scales.

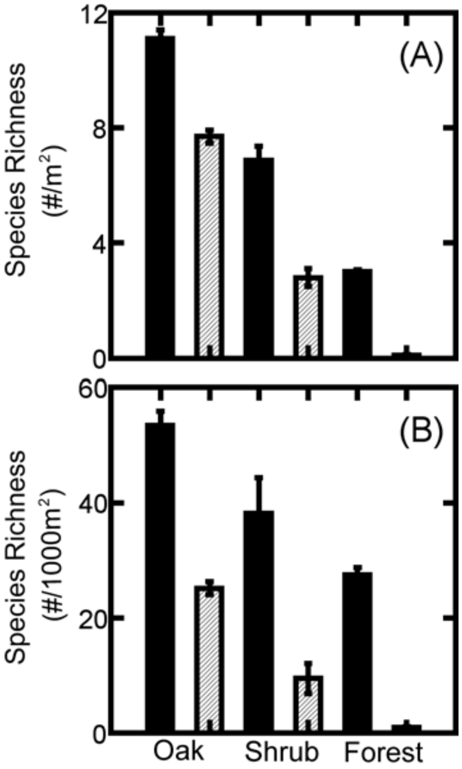

Figure 2—Total species richness (solid bars) and alien species (hatched bars) at the (A) 1-m^2 and (B) 1,000-m^2 scales in oak savanna (440-680 m), chaparral shrubland (860-1,280 m) and coniferous forests (1,400-2,400 m) in the southern Sierra Nevada.

These vegetation types differed greatly in the dominant life history type. Annuals dominated the blue oak savannas, both in terms of species *(fig. 3A)* and cover *(fig. 3B)*, and the bulk of these annuals were grasses *(fig. 3C)*.

The blue oak savannas differed from other communities in a number of soil parameters. They had a significantly lower sand content *(fig. 4A)*, markedly higher phosphorous levels *(fig. 4B)*, and substantially lower surface litter *(fig. 4C)*. Other soil parameters (pH, NO_3, NH_4, K) did not vary significantly between these vegetation types.

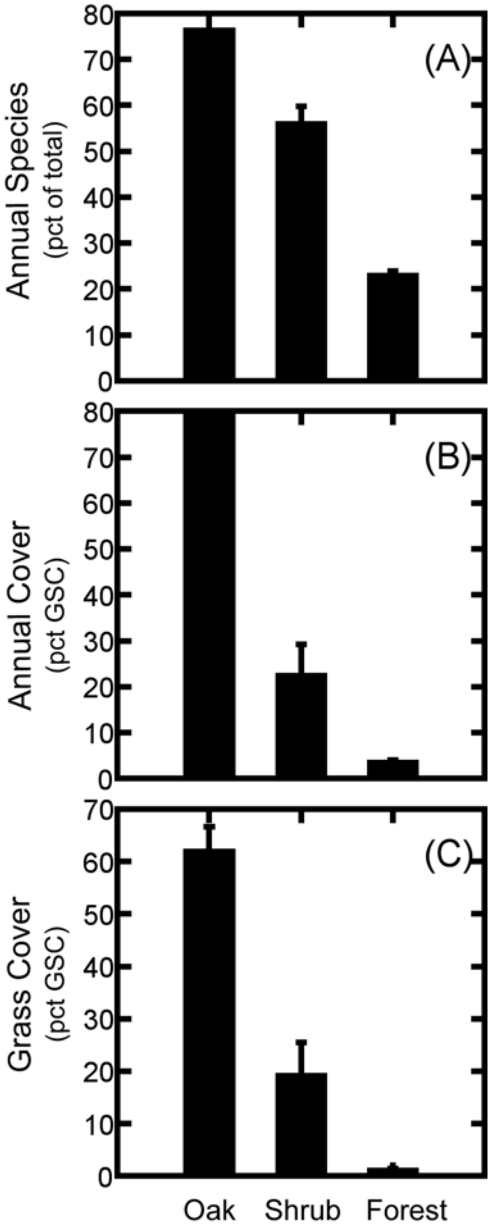

Figure 3—Annual species as (A) percentage of the total flora and (B) cover and (C) grass cover in blue oak savanna, chaparral and coniferous forests in the southern Sierra Nevada. Vegetation types with the same letter above the bar were not significantly different at (*P*>0.05; i.e., all bars are significantly different), middle line indicates the standard error.

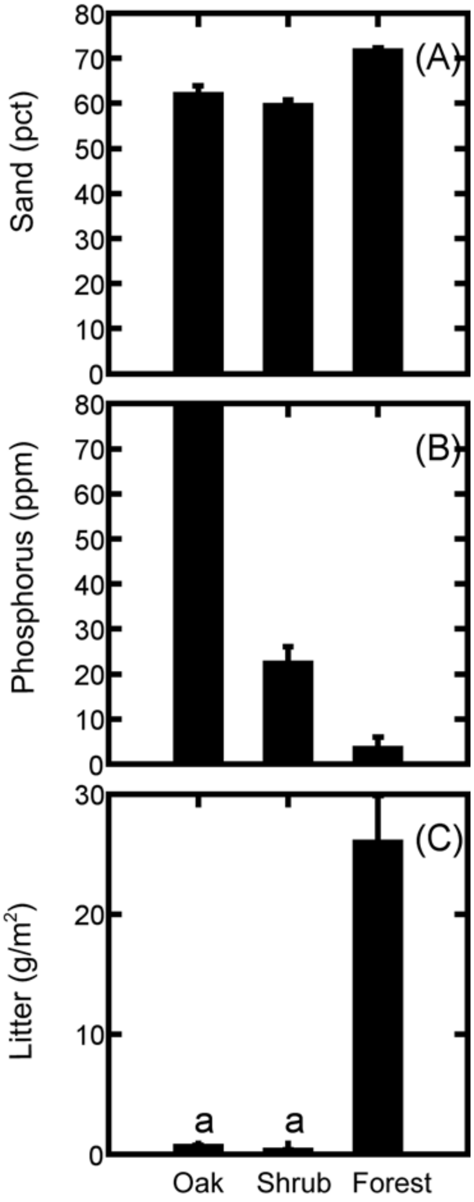

Figure 4—Comparison of soil characteristics between blue oak savanna, chaparral and coniferous forests in (A) percentage sand, (B) phosphorous content and (C) surface litter. Vegetation types with the same letter above the bar were not significantly different at ($P>0.05$), middle line indicates the standard error.

Grazing Impacts on Blue Oak Savannas

Species richness in the blue oak savanna sites ranged from an average of 10-15 species per m^2 to 50-60 species per 1,000 m^2 *(fig. 5)*. Grazing history in the blue oak savanna tended to increase total species richness at all scales but this was not statistically significant ($P>0.05$, $n=5$). The scaling relationship between species richness and area was similar between grazed and non-grazed sites. All exhibited a substantially better fit to a log-log regression (r^2=0.90, 0.83, 0.96, for control, cattle, and horse grazed, respectively) than a semi-log regression (r^2=0.75, 66, 84) and all deviated slightly from a linear relationship by being slightly depauperate in species richness at the intermediate scale *(fig. 5)*.

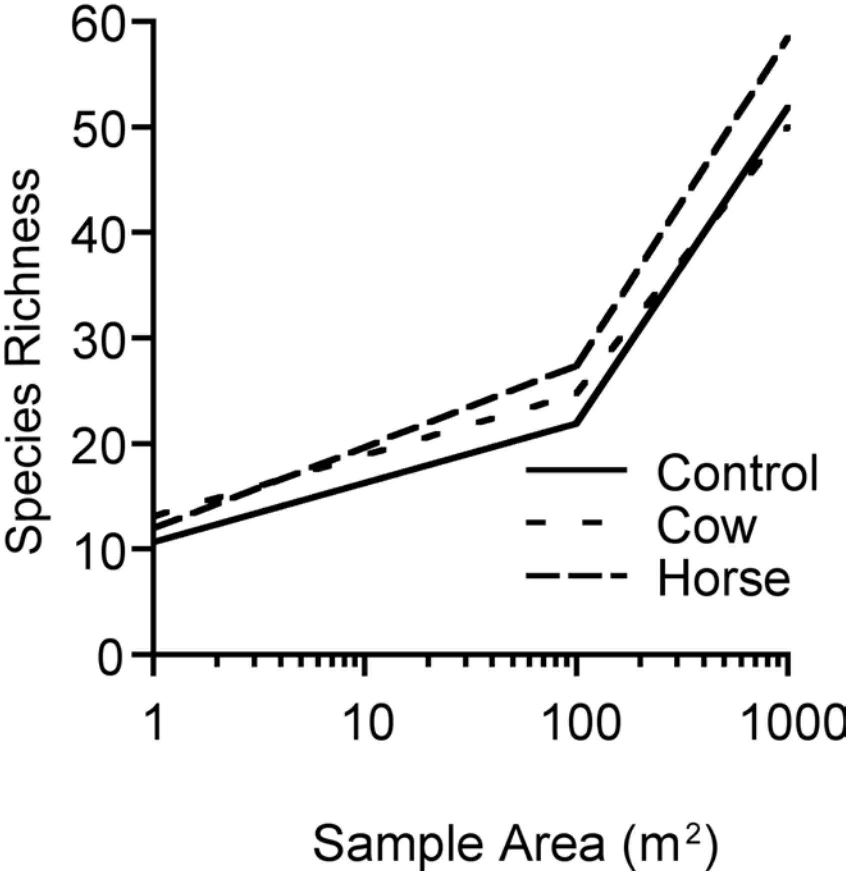

Figure 5—Log-log species area curves for blue oak savanna "controls" (no livestock grazing), cattle grazed, and horse grazed sites, based on nested plots.

Grazing did not significantly affect total cover (P>0.05, n=5) but there were differences in proportions of growth (and possibly functional) forms. Grass cover was significantly greater on horse grazed plots (P<0.05, n=5) and the density of herbaceous perennials was higher on the cattle grazed plots (P<0.05, n=5). In addition, grazing had a statistically significant impact on alien species richness *(fig. 6A and 6B)* and cover *(fig. 6C)*. Cattle grazed pastures had a greater proportion of their cover and flora contributed by aliens than did horse grazed pastures, although this was only significant at the 1-m^2 scale.

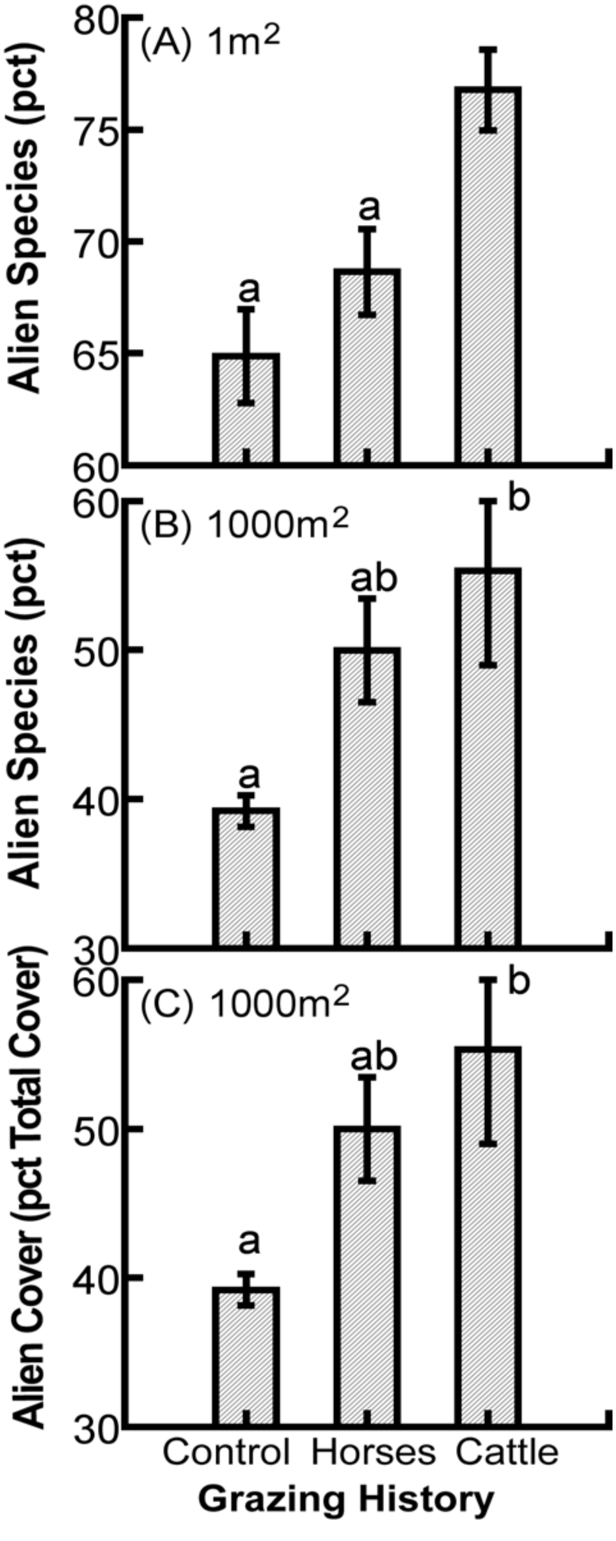

Figure 6—Impact of horse and cattle grazing on alien species richness at (A) 1-m^2 and (B) 1,000-m^2 and (C) proportion of total cover contributed by alien species. Treatments with the same letter above the bar were not significantly different at (P>0.05), middle line indicates the standard error.

The dominant natives on most blue oak sites were forbs: *Amsinckia menziesii, Claytonia perfoliata, Holocarpha heermannii, Plagiobothrys nothofulvus,* and *Trifolium microcephalum.* In contrast, the dominant aliens were mostly grasses: two species of *Avena,* seven species of *Bromus,* predominantly *B. diandrus* and *B. hordeaceous,* two species of *Hordeum, Lolium multiflorum* and *Vulpia myuros*; although some alien forbs were dominant as well: C*entaurea melitensis, Geranium molle, Cerastium glomeratum*, four species of *Erodium, Silene gallica,* and two species of *Torilis*). The total alien flora recorded from the blue oak savanna sites comprised 56 species, all of which were annuals. Of the total alien flora, 10 species showed significant differences in response to grazing pressure *(fig. 7)*. Horse or cattle grazed sites were dominated by alien annual grasses such as *Bromus diandrus, Hordeum murinum,* and *Vulpia myuros.* Control sites had significantly greater cover by alien forbs, particularly *Geranium molle, Hypochoeris glabra,* and *Trifolium dubium.*

Discussion

Relative to chaparral shrublands and coniferous forests, blue oak savannas in the southern Sierra Nevada foothills are markedly different, not only in physiognomy, but in diversity and magnitude of alien plant invasion. While this pattern comes as no surprise to those familiar with this region, the causal factors have not been widely explored.

Most of the diversity in these oak savannas is contributed by annual species and thus the low overstory canopy levels are important in allowing the persistence of these heliophylic (light-loving) species. In associated shrublands and forests, open canopies are a temporary phenomenon due to fires and thus high light conditions favoring annuals are transient habitats that require frequent colonization. The species-rich flora of annual genera in the California Floristic Province (Raven and Axelrod 1978) is likely one important factor in the higher diversity of blue oak savannas.

The extraordinary alien flora in the understory of blue oak savannas is striking, particularly when contrasted with the limited invasion of associated communities. The transient open canopy conditions in other communities may explain the lack of alien annuals but do not stand as an adequate explanation for fewer aliens per se. Past and present human activities may explain some of this pattern. The majority of invasive species in California have their origins in the Mediterranean Region, including southern Europe, North Africa, and Eurasia (Shmida 1981), where they potentially have been in association with anthropogenically altered landscapes through a significant portion of the Holocene (Atherden and Hall 1999). Valleys and foothills in the Old World have had the longest history of intensive land use and present the greatest opportunity for co-evolution with human-perturbed landscapes. In California, these valley and foothill habitats were also the ones most immediately and thoroughly exploited by Europeans, creating favorable sites for the establishment of exotics pre-adapted to such disturbed landscapes.

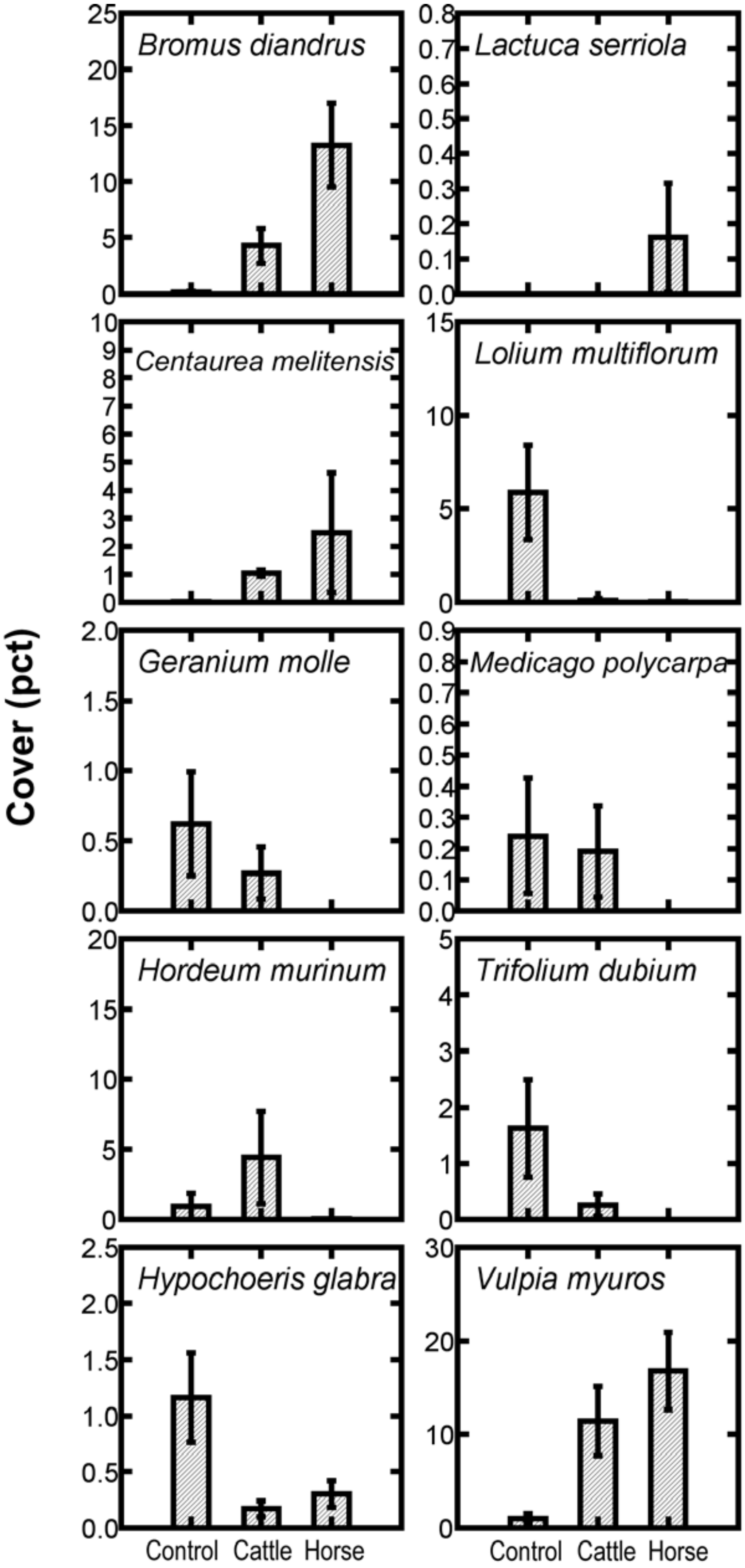

Figure 7—Alien species with cover significantly affected by grazing in blue oak savannas (lines indicate standard errors).

The present dominance of blue oak savannas by alien species raises a number of interesting questions. At the scale of 1-m^2, the majority of species are aliens *(fig. 2A)* and nearly half of the flora at each site is composed of aliens *(fig. 2B)*. Either, these oak savannas are much richer in diversity today than prior to EuroAmerican colonization, or these aliens have displaced a large component of the native flora. Commonly it is thought that these aliens, most of which are annual grasses, have displaced native perennial bunchgrasses. If that is true, then in light of the rather limited number of native bunchgrass species in our flora (Hickman 1993), natural diversity prior to EuroAmerican settlement, was much lower. Alternatively, native annuals, of which there is a rich regional flora may have dominated these communities, and thus alien invasion may not have greatly changed species richness.

Another interesting facet of this massive alien invasion of blue oak savannas is its apparent permanence. The controls in this study have not had livestock grazing in at least 100 years and may never have been intensively grazed. These sites also have never been plowed, which is often associated with a more or less permanent alien presence (Stromberg and Griffin 1996) Today the floristic differences between our control sites and the currently grazed sites are rather subtle. Hypotheses that may explain the persistence of the alien flora in these long undisturbed blue oak savannas are: (1) the native flora that formerly made up the understory has been so severely decimated in the region that dispersal is a major limitation to reestablishment, (2) these savannas are an anthropogenic artifact due to accelerated fire frequency that has converted a closed canopy woodland/shrubland into a savanna, and thus elimination of the alien flora requires return to the closed canopy condition, and (3) due to Holocene climatic changes, the more arid adapted alien annual grasses, through pre-adaptation, are better adapted to these sites and consistently out compete the native flora. These are testable hypotheses that await further experimentation.

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Northwest California Oak Woodlands: Environment, Species Composition, and Ecological Status[1]

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Abstract

This paper describes the oak woodland plant communities of Northwest California and their ecological status using data from 446 ecology plots collected on federal lands in Humboldt, Trinity, Siskiyou, Mendocino, Tehama, Glenn, Colusa and Lake Counties. Geographically, oak woodlands lie between the coastal mixed evergreen forests and the valley grasslands of the Central Valley. They were found in small patches nested within a mosaic of annual grasslands and conifer forests, and hence contain species common to both of these vegetation types. The oak woodlands of northwest California were primarily included in three vegetation series: Oregon white oak (*Quercus garryana*), black oak (*Quercus kelloggii*) and blue oak (*Quercus douglasii*). Valley oak (*Quercus lobata*) was also found in the study area, but because of its limited extent and insufficient samples, it will not be described here. Due to their history of grazing and their proximity to annual grasslands, many of the Northwest California oak woodlands contained high cover of non-native species. In some types, non-native grass and/or forb cover far exceeded that of native species. The forb and grass layers differed from one another based on the general shift of moderate overall cover of non-native grasses to native forbs. Species diversity in these oak woodland systems is a controversial subject because of perceived losses of biological diversity. After the introduction of invasive non-native, annual, Mediterranean species, many of the native species were displaced. Species composition of oak woodlands and annual grasslands will be compared with special attention paid to the cover of non-native species. The ecological status of oak woodlands in Northwest California will be discussed from several perspectives. These include species composition of grasses and forbs, comparisons of cover, species counts, annual and perennial species and native and non-native species. The long-term successional status of these systems will be described using assigned seral species status. Noxious and invasive weeds found in these oak woodlands will also be described and compared to annual grasslands.

Introduction

California's oak woodlands play a prominent role in the natural and cultural history of the State (Pavlik and others 1991). They provide shelter and food for wildlife, as well as wood and fuel for humans and feed for livestock. Oak woodlands are key elements of our California biological diversity. They contain some of the highest species diversity found in our native communities (Jimerson and others 2000). Statewide threats to oak woodlands are many, including: urbanization, conversion to agriculture, fragmentation, low rates of regeneration, competition from

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introduced exotic species and sudden oak death. Studies such as this one can help us identify site-specific risks to oak woodlands and help us to develop strategies to combat them.

The northwest California portion of the State's oak woodlands lie geographically between the coastal mixed evergreen forests and the valley grasslands of the Central Valley (Griffin 1988). They were found in small patches (averaging 29.3 acres/patch), nested within a mosaic of annual grasslands (Jimerson and others 2000) and conifer forests, and hence contain species common to both of these vegetation types. Their extent on National Forest lands within the study area has been estimated at over 725,000 acres. This paper will describe the oak woodland plant communities of Northwest California along with their ecological status and compare them to the annual grasslands found in close proximity.

Methods

The study area included the National Forest lands in Humboldt, Trinity, Siskiyou, Mendocino, Tehama, Glenn, Colusa and Lake Counties. Vegetation maps, past vegetation sampling and local knowledge of oak woodland locations were used to stratify the study area. Four hundred and forty-six plot samples were collected throughout the study area. Only federal lands were sampled for purposes of this study, which reduced the quantity of blue oak woodlands available for sampling.

Sampling methods followed the USDA Forest Service protocol (Allen 1987, Allen and Diaz 1986) used in earlier vegetation classifications completed in northwest California (Jimerson 1994, Jimerson and others 1995, Jimerson and others 1996). These methods included identification of all species for each stratum (tree, shrub, forb and grass) along with their cover and density. Species nomenclature followed Hickman (1993). Environment was described for all plots (location, elevation, aspect, slope, micro-position and landform) and selected plots had soil profiles described (parent rock, soil type, depth, texture, coarse fragments, diagnostic horizons).

Classification methods followed earlier studies in Northwest California (Jimerson 1994, Jimerson and others 1995, Jimerson and others 1996). Initial classification was accomplished using the polythetic divisive classification technique, Two-way Indicator Species Analysis (TWINSPAN) (Hill 1979). TWINSPAN was paired with the ordination techniques Detrended Correspondence Analysis (Hill 1979) and Canonical Correspondence Analysis (Ter Braak 1992) to define the final classification. The final veg types were compared using discriminant function analysis (DFA) (Jennrich and Sampson 1985) to identify the significant environment variables that distinguish each veg type from one another.

Species diversity assessment is a tool in the examination of plant communities and their ecological context. We believe it is a necessary part of this classification analysis and will discuss it here at various scales, particularly in light of 1) the controversy surrounding the effects of non-native species on native species diversity, and 2) the utility of classification as a tool in managing for the maintenance of species diversity.

Species diversity is composed of two components: (1) richness (the total number of species), and (2) evenness (how the data are distributed among the species) (Ludwig and Reynolds 1988). These diversity measures were calculated for each plot using the program PC-ORD (McCune and Mefford 1999).

Oak woodlands and annual grasslands have differing degrees of non-native plant invasion that are primarily limited to herbaceous species (Saenz and Sawyer 1986). Annual grasses are the primary non-native invaders of oak woodlands, although a few non-native forbs are important invaders as well. These non-native invaders have the potential to alter ecological relationships and processes (Mooney and others 1986).

The ecological status of northwest California oak woodlands can be described from several perspectives. First, comparisons can be made of cover and species counts of grasses versus forbs, annuals versus perennials and native versus non-native species using one-way analysis of variance (SPSS Inc. 2000). Second, plant species are often used as indicators of ecological status (early, mid or late seral) since they tend to reflect site potential, site history and past management activities (USDA 1997). Species are designated here as indicators of early-seral, mid-seral or late-seral conditions as defined below:

- Early-seral species are associated with very disturbed or young associations (pioneer species), with low abundance in stable associations, but invasive with high abundance in unstable associations (examples, *Aira caryophyllea*, *Briza minor*, and *Cynosurus echinatus*).
- Mid-seral species abundance increases significantly with increased disturbance and maintains high abundance in recovered, stabilizing associations (examples, *Danthonia californica*, *Elymus glaucus*, and *Poa pratensis*).
- Late-seral species are typically found in undisturbed associations that decrease or maintain low abundance with increased disturbance (examples, *Achnatherum lemmonii*, *Festuca idahoensis*, and *Melica harfordii*).

Oak woodland ecological status will be assessed by combining the factors described above. For example, sites with high cover of annual and perennial, non-native species, in early-seral states would point toward a low ecological status. In contrast, those sites with high cover of perennial, native species, in late-seral states would be described as in a high ecological status.

Results

Vegetation Series

The classification of 446 oak woodland plots in northwest California identified three primary vegetation series: Oregon white oak (*Quercus garryana*), black oak (*Quercus kelloggii*) and blue oak (*Quercus douglasii*). They were found in nearly pure stands dominated by white oak, black oak or blue oak, or in association with other tree species such as Douglas-fir (*Pseudotsuga menziesii*), Ponderosa pine (*Pinus ponderosa*), gray pine (*Pinus sabiniana*), canyon live oak (*Quercus chrysolepis*), California buckeye (*Aesculus californica*) and bigleaf maple (*Acer macrophyllum*). Collectively these woodland communities fit under what Griffin (1977) called the northern oak woodlands. Previous oak woodland plant community classification in northwest California and southwest Oregon was completed by Atzet and others (1996), Jimerson and others (1988), Leitner and Leitner (1988), Parker and Matyas (1979), Reigel and others (1991), Stuart and others (1996), and Sugihara and others (1987). Currently, the plot data collected in this study is being described in a plant association classification for oak woodlands in northwest California.

The northwest California oak woodland series were compared using discriminant function analysis (DFA) (Jennrich and Sampson 1985) to identify the significant environmental variables that distinguish each series from one another. Highly significant variables are compared by series in *table 1.* Precipitation is a key discriminant variable, highest in the black oak series and significantly lower in the blue oak series. Since rainfall in northwest California decreases from west to east and north to south, the black oak series was more often found on more westerly sites in the northern portion of the study area, while the blue oak series was found on the most inland sites in the southern portion of the study area. The white oak series, on the other hand was found throughout the study area.

Table 1—*Mean significant discriminant function analysis (dfa) variables identified in the oak woodland series comparison (df 2, 417).*

Variables	White oak	Black oak	Blue oak	f	dfa axis	sign.
Precip. (in.)	54.4	60.7	47.9	11.5	dfa 1	.001
Distance to ocean (mi.)	46.3	68.4	64.4	46.5	dfa 2	.001
North/south gradient	4498862.1	4508568.2	4405248.4	16.2	dfa 1	.001
Summer precip. (index)	7.7	7.8	7.2	27.2	dfa 1	.001
Slope (pct)	41	37	28	3.3	dfa 2	.038
Elevation (ft.)	3,217	3,184	2,229	7.5	dfa 2	.001
Forb cover (pct)	15	13	23	3.5	dfa 1	.030
Grass cover (pct)	33	18	43	23.8	dfa 1	.001
Tree cover (pct)	59	70	47	11.6	dfa 2	.001
Radiation index	.494	.478	.354	2.7	dfa 2	.010

Inland blue oak sites had the lowest tree cover, highest forb cover, highest grass cover and lowest elevation of the three oak woodland series. In contrast, the black oak series was found on sites with the highest mean rainfall, in the northern portion of the study area, on cool upland sites. These three factors help explain why black oak has the highest mean tree cover of the three oak woodland series. The white oak series generally was found on the highest elevation, warmest sites, with the highest mean slope.

The variables displayed in *table 1* largely explain the gross physical and environmental variability in oak woodland series field plots. Axis 1 (dfa 1) explained 56 percent of the variance in the oak woodland series, while axis 2 explained 44 percent of the variance. The highest correlation of each variable to a dfa axis is listed in *table 1.* The test of the hypothesis that the group centroids for dfa axis 1 and 2 were equal was rejected (chi-square 272.7, df 42, sign. 0.001). In other words the two discriminant functions differ significantly from one another.

The key species identified in the Detrended Correspondence Analysis (DCA) (Hill 1979) that best describe the plant communities and explain the environment variability in each series are described below in *table 2.* These species are closely related to key environment gradients. For instance, Douglas-fir was found on mesic sites within the white oak and black oak series, while California buckeye occupies warm, dry sites. Bigleaf maple was only found on moist, cool sites in the black oak series. Gray pine was most often found on soils derived from serpentine parent material. In the shrub layer, California juniper (*Juniperus californica*) was only found on harsh, dry, rocky, inland sites. In contrast, mock orange (*Philadelphus lewisii*) and hazelnut (*Corylus cornuta var. californica*) were only found in shaded, cool, riparian locations near streams. Grass layer indicator species include tall oat grass (*Arrhenatherum elatius*), which had its most extensive occurrence in the western part of the study area on cool, moist sites in close proximity to the Pacific Ocean. Hedgehog dogtail (*Cynosurus echinatus*) was found throughout the southern part of the study area on sites heavily disturbed by cattle. Blue wild-rye (*Elymus glaucus*) and California fescue (*Festuca californica*) appeared to have their highest abundance on sites with high canopy cover.

Table 2—*Tree, shrub and grass indicator species identified in each oak woodland series. X indicates presence.*

Species	Life form	White oak series	Black oak series	Blue oak series
Quercus garryana	tree	X	X	X
Pseudotsuga menziesii	tree	X	X	
Pinus ponderosa	tree	X	X	
Quercus chrysolepis	tree	X	X	
Pinus sabiniana	tree	X	X	X
Aesculus californica	tree	X		
Acer macrophyllum	tree		X	
Juniperus californica	shrub			X
Arctostaphylos patula	shrub	X		
Rhus diversiloba	shrub	X	X	X
Cercocarpus betuloides	shrub	X	X	
Ceanothus cuneatus	shrub	X	X	
Quercus garryana var. *breweri*	shrub	X	X	
Quercus wislizenii var. *frutescens*	shrub		X	
Corylus cornuta	shrub		X	
Philadelphus lewisii	shrub	X		
Arrhenatherum elatius	grass		X	
Bromus carinatus	grass			X
Vulpia microstachys	grass			X
Cynosurus echinatus	grass	X	X	X
Festuca californica	grass	X	X	
Melica harfordii	grass	X		
Elymus glaucus	grass	X	X	

Some of the species listed in *table 2* are indicators of altered disturbance regimes. For instance, high cover of Douglas-fir under an oak canopy is an indication of an altered fire regime. Northwest California oak woodlands would naturally be subjected to frequent low intensity fires that tend to kill invading Douglas-fir seedlings and saplings. Over the last 50 years the USDA Forest Service has practiced an aggressive fire suppression policy. The effect of this was an increase in cover of Douglas-fir on oak woodland sites. This can lead to the development of fuel ladders into the oak canopy that increase the potential for stand replacing fire and a reduction in forb and grass species diversity by shading. A second example involves hedgehog dogtail; this aggressive alien grass increases in cover on sites that have been over-grazed. Because of the open nature of this plant, it can affect soil cover and lead to increased surface erosion and reductions in species diversity. Tall oatgrass is an example of a non-native perennial grass species introduced in order to control bank erosion. This species can grow to seven feet in height and shade out native species through its tall stature and production of smothering thatch (Jimerson and others 2000).

Species Richness

A species richness comparison of annual grasslands, meadows, chaparral and oak woodlands found significant differences by vegetation type (Jimerson and others 2000). The oak woodland vegetation type had significantly higher richness (X=25.3 species/plot) than any other type.

Table 3—*Oak woodland series comparison of mean species life form counts.*

Life form	Oak woodland series	Mean species count	Std. error
Forb native	white oak	9.4	0.51
	black oak	7.5	0.56
	blue oak	11.5	1.21
	overall	8.8	0.37
Forb non-native	white oak	1.2	0.09
	black oak	1.0	0.11
	blue oak	2.9	0.51
	overall	1.2	0.07
Grass native	white oak	2.9	0.20
	black oak	2.2	0.20
	blue oak	3.7	0.49
	overall	2.7	0.14
Grass non-native	white oak	2.0	0.12
	black oak	1.5	0.12
	blue oak	4.6	0.62
	overall	1.9	0.10

A species richness comparison by oak woodland series also found significant differences (df=2, F=15.74, sig= 0.001). The highest mean number of species was found in the blue oak series (29.8 species/plot), while the lowest mean species richness was found in the black oak series (23.1 species/plot). A comparison of species counts by oak woodland series *(table 3)* shows the same trends. The blue oak series had significantly higher species counts (P=0.001) by lifeform than the white oak and black oak series. It appears that these differences in species richness are related to overstory tree canopy closure. For instance, when canopy closure was high, species richness was low and when canopy closure was low, species richness was high. This is exemplified by the high mean canopy closure found in the black oak series (73 percent cover), and its associated low species richness. The blue oak series, on the other hand, has low tree canopy closure (53 percent) and high species richness.

Species Diversity

The oak woodland samples indicate a relatively plant species rich environment when compared to other Northwest California vegetation series. A total of 714 species were identified from 446 ecology field plots. This included 28 tree, 106 shrub, 493 forb and 87 grass and grass-like species.

Thirty-four percent of the grass species identified were annuals and 66 percent were perennials. Ninety percent of the annual grasses were non-native. These included silver hairgrass (*Aira caryophyllea*), slender wild oat (*Avena barbata*), common wild oat (*Avena fatua*), soft chess (*Bromus hordeaceus*), hedgehog dogtail, and six-weeks fescue (*Vulpia myuros*). Of the perennial grasses, 82 percent were native species, including California brome (*Bromus carinatus*), blue wild-rye, California fescue, Idaho fescue (*Festuca idahoensis*), western fescue (*Festuca occidentalis*), Harford's melic (*Melica harfordii*), Pacific bluegrass (*Poa secunda*) and bottlebrush squirreltail (*Elymus elymoides*).

The forb layer had the same ratio of annual to perennial species as the grass layer. Thirty-four percent of the forbs identified were annuals and 66 percent were perennials. Seventy-nine percent of the annual forbs were native; they included California hedge parsley (*Yabea microcarpa*), miner's lettuce (*Claytonia perfoliata*), Clarkia (*Clarkia rhomboidea*), goose grass (*Galium aparine*), common madia (*Madia elegans*), slender tarweed (*Madia gracilis*), sweet cicely (*Osmorhiza chilensis*) and tonella (*Tonella tenella*). Important non-native forb species included the thistles (*Cirsium* spp.) and European hedgeparsley (*Torilis arvensis*). Of the perennial forbs, 95 percent were native species; including common yarrow (*Achillea millefolium*), spearleaf agoseris (*Agoseris retrorsa*), soap root (*Chlorogalum pomeridianum*), Collomia (*Collomia grandiflora*), Pacific houndstongue (*Cynoglossum grande*), white hawkweed (*Hieracium albiflorum*), iris (*Iris* spp.), wild pea (*Lathyrus* spp.), swordfern (*Polystichum munitum*), western buttercup (*Ranunculus occidentalis*), purple sanicle (*Sanicula bipinnatifida*), gembleweed (*Sanicula crassicaulis*), American vetch (*Vicia americana*) and Shelton's violet (*Viola sheltonii*).

Existing Conditions

Vegetation cover in the oak woodlands was usually high when compared to other vegetation types in Northwest California. The tree layer accounted for 64 percent mean cover, shrub layer 22 percent, grass layer 26 percent and forb layer contributed an additional 14 percent mean cover. Grass cover was evenly split between native (14 percent) cover and non-native species (13 percent). Native cover consisted of 13 percent perennial and 1 percent annual species *(table 4).* Non-native cover consisted of 11 percent annual and 2 percent perennial species. This shows the effects of long-term competition from aggressive non-native species introduced to these sites through livestock grazing.

The forb layer, on the other hand, had a mean cover of 10 percent natives compared to non-native cover of 2 percent *(table 4).* Annual and perennial native species accounted for 3 percent and 7 percent mean cover, respectively. However, the annual native forb category differed significantly by vegetation series (P=0.001). Non-native forb species were much reduced, contributing 2 percent annual and < 1 percent perennial forb cover. Both of these categories differed significantly (P=0.001) between vegetation series.

Table 4—*Comparison of lifeform cover percent for forbs and grasses in oak woodlands and annual grasslands.*

Life form	Oak woodlands pct. cover (std. er.)	Annual grasslands pct. cover (std. er.)
Forb annual native	3.2 (0.2)	24.1 (1.5)
Forb annual non-native	1.8 (0.2)	7.3 (0.9)
Forb perennial native	6.9 (0.3)	8.7 (0.6)
Forb perennial non-native	0.4 (0.1)	3.6 (0.4)
forb native	10.1 (0.5)	32.8 (1.3)
Forb non-native	2.2 (0.2)	10.9 (0.7)
Total forb cover	12.3 (0.8)	43.7 (1.4)
Grass annual native	0.3 (0.1)	0.2 (0.1)
Grass annual non-native	11.2 (0.8)	57.0 (1.8)
Grass perennial native	13.4 (0.9)	5.4 (0.8)
Grass perennial non-native	1.7 (0.4)	5.7 (1.0)
Grass native	13.7 (0.9)	5.6 (0.7)
Grass non-native	12.8 (0.9)	63.7 (1.5)
Total grass cover	26.5 (1.2)	69.3 (1.4)

In a lifeform comparison between oak woodlands and annual grasslands *(table 4),* significant differences were found in several categories. Annual grasslands had significantly higher cover in all forb categories and in non-native annual and perennial grasses. In contrast, oak woodlands had higher cover of native perennial grasses.

Seral Status

The seral status of Northern California oak woodlands is a living record of disturbance, i.e. grazing, fire, drought and competition from invasive species. Overall, the oak woodland plot samples were dominated by low mean grass cover in both the early-seral (8 percent) and late-seral stages (10 percent), with less grass cover in the mid seral stage (4 percent) *(table 5).* This is in stark contrast to the annual grasslands where overall early seral cover (61 percent) far exceeded all other seral stages *(table 5).* In reference areas, where disturbance was primarily natural and cattle grazing was absent, the grass seral status was often dominated by cover in the late seral category. When the current seral status is compared to these reference areas, it points toward an overall conclusion that some of our northwest California oak woodland communities are now in a non-equilibrium condition; i.e., are very disturbed or young associations dominated by invasive species.

When the seral status was analyzed by oak woodland series, significant differences were found between series for early seral grass cover (P=0.001) and late-seral cover (P=0.001) *(table 5).* The blue oak series had the highest early-seral cover (32 percent) followed by the Oregon white oak series (10 percent). There was no significant difference in mid-seral grass cover. Late-seral cover was highest in the Oregon white oak series (14 percent), followed by the blue oak (8 percent) and black oak series (6 percent).

Table 5—*Mean percent grass cover and standard error for seral state by oak woodland series.*

Vegetation series	Early-seral pct mean	Early-seral pct std. error	Mid-seral pct mean	Mid-seral pct std. error	Late-seral pct mean	Late-seral pct std. error
Oregon white oak	10.3	1.1	4.3	0.6	14.2	1.4
Black oak	4.6	0.9	2.7	0.5	5.9	0.8
Blue oak	31.9	4.7	6.2	3.9	7.9	2.7
Oak woodlands (all)	8.1	0.7	3.6	0.4	9.9	0.8
Annual grasslands	61.5	1.9	2.8	0.5	2.4	0.6

Forb cover was found to be significantly different for all seral stages by oak woodland series and in a comparison to annual grasslands. However, I believe that only the early-seral category (P=0.001) was ecologically significant because of the very low mid seral and late seral cover in each series. Early-seral forb cover was higher in the blue oak series (15 percent) than the Oregon white oak series (6 percent) and black oak series (4 percent) *(table 6).*

Table 6—*Percent mean forb cover and standard error for seral state by oak woodland series.*

Vegetation series	Early-seral pct mean	Early-seral pct std. error	Mid-seral pct mean	Mid-seral pct std. error	Late-seral pct mean	Late-seral pct std. error
Oregon white oak	6.2	0.5	5.0	0.3	2.5	0.2
Black oak	4.1	0.4	3.2	0.3	1.8	0.2
Blue oak	15.1	3.7	6.8	1.6	1.9	0.4
Oak woodlands (all)	5.4	0.3	4.2	0.2	2.2	0.1
Annual grasslands	30.0	1.4	9.5	0.7	4.1	0.6

Noxious and Invasive Weeds

The noxious and invasive (invasive) weeds identified in the northwest California oak woodlands and annual grasslands are displayed in *table 7.* Overall, invasive weeds occurred relatively infrequently in oak woodlands (27 percent of the plots) when compared to annual grasslands. Twelve percent of plots contained only 1 percent invasive weed cover, with an additional 9 percent of the plots containing 2-5 percent cover. The remaining plots (6 percent) contained 6-22 percent invasive weed cover. This is in sharp contrast to the annual grasslands where 78 percent of the plots were found to contain invasive weeds (Jimerson and others 2000). Invasive weed cover on annual grasslands included 15 percent of the plots with 1 percent cover, 21 percent with 2-5 percent cover, 27 percent with 6-20 percent cover and 14 percent of the plots with 21-95 percent cover. Clearly, invasive weed cover in annual grasslands was significantly higher than in oak woodlands and is likely related to continued disturbance from cattle grazing. Unfortunately, because of the proximity of annual grasslands to oak woodlands, they provide a potential threat of invasive weed invasion into oak woodlands. Also, cattle tend to rest in the shade of oak woodlands and both ruminate and defecate in place, serving as a vector for these weeds.

Noxious and invasive weed species composition in oak woodlands and annual grasslands was almost identical, only the frequency of occurrence and percent cover differed. Cheatgrass (*Bromus tectorum*) had the highest frequency of occurrence in both oak woodlands (20 percent) and annual grasslands (45 percent). Medusahead (*Taeniatherum caput-medusae*) was second in frequency of occurrence, 26 percent in the annual grasslands and < 1 percent in oak woodlands. Klamathweed (*Hypericum perforatum*) was third in frequency of occurrence. It was found in 15 percent of the annual grassland plots and 4 percent of the oak woodlands. Yellow starthistle (*Centaurea solstitialis*) was found in 8 percent of the annual grasslands and 2 percent of the oak woodlands. Bull thistle (*Cirsium vulgare*) was the only invasive weed found with higher frequency in the oak woodlands (5 percent), compared to annual grasslands (1 percent) *(table 7)*. The shade intolerance of most of these species acts as a limiting factor to their success in oak woodlands.

No significant difference (P=0.175) in invasive weed cover was found by oak woodland series. However, when plant associations within the series were compared, significant differences in invasive weed cover were noted (P=0.001). Plant associations containing gray pine and hedgehog dogtail had higher frequencies of invasive weed occurrence than all other types.

Oak woodland sites containing noxious and invasive weeds had significantly higher bare ground (P=0.05), higher surface gravel and rock cover (indicative of disturbed surfaces) (P=0.009), thinner A horizons (P=0.017), lower available water holding capacity (P=0.05), as well as lower canopy cover (P=0.001) and higher cover of early seral grass species (P=0.002). These attributes increase the potential for successful noxious and invasive weed encroachment.

The low frequency and cover of invasive weeds in oak woodlands is likely due to the low extent of surface disturbance and higher canopy cover, particularly when compared to annual grasslands. Management that maintains high litter cover or limits the development of bare ground will likely reduce the potential for new infestation sites. Where small colonies exist, they can be controlled through a variety of strategies. These might include direct removal of plants, use of fire, biological controls, seasonally timed, close livestock grazing, and use of herbicides.

Table 7—*List of noxious and invasive weeds found in northwest California oak woodlands and annual grasslands, including frequency of occurrence.*

Layer	Species name	Oak woodlands pct of plots	Annual grasslands pct of plots
Forb	*Centaurea melitensis*	0.2	1
Forb	*Centaurea solstitialis*	2	8
Forb	*Cirsium vulgare*	5	1
Forb	*Convolvulus arvensis*	0.2	4
Forb	*Euphorbia* sp.	0.2	0
Forb	*Hypericum perforatum*	4	15
Forb	*Melilotus alba*	0.5	0
Forb	*Mentha pulegium*	0.7	0.5
Forb	*Verbascum thapsus*	1	0
Grass	*Bromus tectorum*	20	45
Grass	*Taeniatherum caput-medusae*	0.7	26

Discussion/Conclusions

The oak woodlands of northwest California were found to be dominated by white oak, black oak or blue oak. They were found in near pure to mixed stands that had high diversity in species, particularly in the forb and grass layers. This was reflected in some of the highest species richness found in the northwest corner of the State. Specifically, oak woodlands had significantly higher species richness than annual grasslands, meadows or chaparral vegetation types. Species richness in oak woodlands appeared to be influenced by overstory canopy cover and was highest in the blue oak woodlands, the vegetation series with the lowest mean canopy closure.

The oak woodland series were arrayed along moisture and temperature gradients that included precipitation, distance to the ocean, position along the north/south gradient, summer precipitation, slope percent, elevation and radiation index. These significant environmental variables best explained the diversity in the oak woodland series.

The oak woodlands had both higher cover of native grasses and lower cover of non-native grasses when compared to annual grasslands. In contrast, the oak woodland forb layer had lower cover of both natives and non-native species. Overall, oak woodlands had low cover in both late and early seral grass and forb species. However, oak woodland seral status was much higher than for annual grasslands, where most of the cover was in early seral species.

Oak woodlands had a much lower frequency of invasive weeds when compared to annual grasslands. If treated while their numbers remain low, they have a much higher potential for control than in annual grasslands. Overall oak woodland ecological status would be rated as moderate due to the near equal cover of grasses in the native and non-native species categories and the variable early seral cover and low late seral cover of both forbs and grasses. However, when oak woodlands are compared to annual grasslands, oak woodlands are clearly in a much higher ecological state because of their higher ratio of native to non-native species and lower cover of early seral species. The same conclusion was drawn in the comparison of invasive weed cover in oak woodlands and annual grasslands.

Although site specific threats to northwest California oak woodlands are fewer than those identified in annual grasslands, several were identified in this study. These include:

- Potential loss in biodiversity as a result of competition from invasive non-native species and understory invasion by conifer species;
- Potential soil productivity loss as a result of surface disturbance from livestock grazing and non-native grass species invasion;
- Increased cover of noxious weeds in conjunction with b; and
- Potential negative impacts on ecological processes through altered fire regimes.

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Leaf Area Index, Leaf Mass Density, and Allometric Relationships Derived From Harvest of Blue Oaks in a California Oak Savanna[1]

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Abstract

Given the key role played by biogenic volatile organic compounds (BVOC) in tropospheric chemistry and regional air quality, it is critical to generate accurate BVOC emission inventories. Because oak species found in California often have high BVOC emission rates, and are often of large stature with corresponding large leaf masses, oaks may be the most important genus of woody plants for BVOC emissions modeling in California airsheds. Accordingly, reference data for leaf mass and leaf area for a stand of native blue oaks were obtained through harvest of 14 trees located in the Sierra Nevada foothills. In addition, leaf mass estimation methods based on a volumetric method and allometric relationships were evaluated for these trees. Leaf mass density (leaf mass per surface area of land) was 310 g m^{-2} for the site, but consideration of the surrounding grassland devoid of trees would result in a value of about 150 g m^{-2}, less than half of reported values for eastern U.S. oak woodlands, but close to a reported value for oaks found in an Italian site, which like California has a Mediterranean climate. The mean value for leaf area index (LAI) for the 14 individual trees at this oak site was 4.4 m^2 m^{-2}. LAI for the site was 1.8 m^2 m^{-2}, but this value was appropriate for the oak grove only; including the surrounding open grassland would result in an overall LAI value of 0.9 m^2 m^{-2} or less. A volumetric method worked well for estimating the leaf mass of the oak trees. Among allometric relationships investigated, trunk circumference, mean crown radius, and crown projection were well correlated with leaf mass. BVOC estimates based on data obtained at the study site indicate blue oaks may be significant contributors of BVOC to California airsheds where this species is plentiful.

Introduction

It is now well known that volatile organic compounds (VOC) are emitted from vegetation, including natural plant communities, urban landscapes, and agricultural crops. An accurate estimate of the magnitude of biogenic VOC (BVOC) emissions relative to anthropogenic VOC emissions may be critical for formulating effective strategies to reduce concentrations of fine particles, ozone, and other secondary air pollutants which affect human health and reduce yields of agricultural crops.

Concern about the possible critical role of BVOC emissions is reinforced by (a) the fact that on average many BVOC are as reactive, or more reactive, in the atmosphere than emissions from mobile or stationary anthropogenic sources (Carter

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1994); and (b) a growing body of research from studies throughout the world suggesting that BVOC can constitute a significant and even dominant contribution to the overall VOC inventory in both regional airsheds and the global atmosphere (Guenther and others 2000, Lenz and others 1997, Seufert and others 1997). For California, modeling studies suggest that development of specific emission control strategies for reducing ambient ozone in certain airsheds is dependent upon estimated emissions of BVOC. These studies showed that emissions of hydrocarbons from vegetation can make the difference between nitrogen oxides vs. VOC emission controls being the most effective in reducing ozone concentrations (Jackson and others 1996). In heavily vegetated airsheds in California, BVOC emissions may limit the effectiveness of VOC control, setting a floor under the reduction in ozone that can be achieved by reducing anthropogenic VOC.

BVOC emission inventories require species-specific data for BVOC emission rates, areal coverage, and leaf mass, and calculated BVOC emissions will be directly proportional to each of these terms. Trees with both high leaf mass and high BVOC emission rates, such as several of the oak species, may be dominant BVOC emitters in California's natural landscapes. For example, in an earlier study in Ventura and Santa Barbara counties (Chinkin and others 1996), a natural oak woodland dominated the biogenic emission inventory, and oaks are the dominant BVOC emitters in the Mediterranean region (Seufert and others 1997).

Considerable attention has been given to determining BVOC emission rates, including proposal of a taxonomic methodology for assigning isoprene and monoterpene emission rates to unmeasured plant species (Benjamin and others 1996), testing of this hypothesis through emission measurements of additional species (Karlik and Winer 2001a, Winer and Karlik 2001), and further emission characterization of oak species (Csiky and Seufert 1999). However, description of areal coverages of plant species and their leaf masses may currently be the weaker links in BVOC inventory development in California. Quantifying oak distribution and leaf mass is of particular interest for such inventories, as is development of methods for leaf mass estimation useful in field surveys.

The principal goals of the present study were to develop data for a stand of native blue oaks for whole-tree leaf mass (g), canopy leaf mass density (LMD) (g m^{-2}), whole-canopy leaf area (LA) (m^{-2}), and leaf area index (LAI) (m^2 m^{-2}), which could subsequently be used as reference values. In addition, leaf mass estimation methods based on a volumetric method and allometric relationships were evaluated for these oak trees.

Experimental Methods

In July 2000, a grove containing 14 blue oak trees (*Quercus douglasii*) was selected on an east-facing slope on private land in the Sierra Nevada foothills near California Hot Springs, approximately 50 miles northeast of Bakersfield. This stand of trees appeared to be representative of blue oaks found in the oak savannas of the foothill areas of the southeastern San Joaquin Valley. The trees had received no cultural attention such as pruning, irrigation, or fertilizer; and had become established from natural acorn dispersion.

A rectangular grid was established in the field by placing 50 m measuring tapes at right angles so as to encompass the crown projections of the 14 trees. The universal transmercator coordinates for the northeast corner of the grid were found with a global positioning system (GPS) receiver (Garmin 12XL) and checked against a second receiver (Magellan GPS 2000), and were 11S 0345696E and 3970295N, with corresponding latitude-longitude coordinates of 35° 51' 53" N and 118° 42' 33" W. The quadrant marked with the measuring tapes opened to the southwest; the compass headings for the baselines were 168° and 258°. Elevation was 975 m measured with a portable altimeter (Pretel Instruments). The trees were numbered, and the position of each tree was noted. Tree dimensions were measured to a precision of 0.1 m. Tree heights were measured with a telescoping pole, and the distance from the ground to the base of the crown was measured with a steel tape. From these measurements vertical crown depth was calculated. Crown radii of trees were measured in the four cardinal directions from the trunk to the average dripline by using a steel tape, and the means were calculated. Trunk circumferences at breast height were also measured with a steel tape, but to a precision of one cm.

Following measurements of standing trees, each specimen was felled with a chain saw approximately five cm above the soil surface, the stump diameter was measured in two directions, and the number of sapwood rings was counted. Each tree was separated in the field into twigs with leaves, branches, and trunk sections. Branches, defined as stems with diameters between two and 10 cm, and trunk sections with diameters greater than 10 cm, were weighed in the field to the nearest gram. The twigs with leaves were transported to the laboratory and all leaves were removed for drying and weighing, and the twigs were also weighed. Leaves were placed in paper bags and dried for approximately two weeks in a vacant greenhouse with daily maximum temperatures of about 65°C and relative humidity less than 20 percent. Bags of leaves were weighed to the nearest even gram on a digital scale and masses summed for each tree. Bags were spot checked to verify complete drying and no decomposition was noticed. To obtain a value for specific leaf area (SLA) (m^2 g^{-1}), area of 50 fresh leaves was measured with a leaf area meter (LiCor), and then these leaves were dried under the same conditions as the rest of the oak leaves and weighed. Samples of trunks, branches, and twigs were also dried to obtain fresh-weight to dry-weight ratios.

Results

Results from Whole-Tree Harvest for Leaf Mass, LMD, LA, and LAI

Blue oak dimensions and leaf masses are given in *table 1.* Total dry leaf mass for the 14 trees was 92.9 kg. Resulting calculated values for tree dimensions such as crown height, crown projection and DBH are seen in *table 2.* Tree no. 1 had extensive dieback and decay resulting in a hollow center; it was excluded from data analysis where trunk diameter was included in allometric equations, but its leafmass and crown dimensions were included in calculations. Based on counts of sapwood rings, the blue oak trees harvested were about 70-180 years old.

Calculated per-tree values for LMD based on crown projection ranged from 410 to 1300 with a mean of 730 g m^{-2} for these blue oak trees *(table 2).* LMD calculated on the basis of total leafmass divided by the sum of areas of crown projection was 720 g m^{-2}, slightly lower than the mean LMD values for the individual trees. The minimum grid dimensions needed to encompass the driplines of all oak crowns were 16.7 x 18.1 m, an area of 302 m^{-2}. The LMD calculated for the site based on total leaf mass divided by this area was 310 g m^{-2}, considered to be the site LMD value. This value may be compared to values (g m^{-2}) for oak woodlands of various locales, including 375 for Atlanta, GA (Geron and others 1995); 375 for the contiguous United States (Lamb and others 1987, 1993); 160 for holm oak (*Q. ilex*) at Castelporziano, Italy (Lenz and others 1997); and 65 and 130 for scrub oak (*Q. dumosa*) in San Diego County (Kummerow and Mangan 1981). However, the oak stand harvested and measured was surrounded by open grassland, and therefore the LMD value of 310 g m^{-2} represents a maximum for that site. If the LMD was calculated on the basis of the area of the grid plus the surrounding grassland, the value would have been approximately half based on observation of tree cover in the vicinity. No quantitative data for oak coverage were available, but a gradation from scattered trees at lower elevations to apparent crown closure on slopes at higher elevations was observed.

Table 1—*Plant dimensions of native blue oak trees selected for harvest and measurement of total dry leafmass.*

Tree (no.)	**Tree height** (m)	**Ground-crown distance** (m)	**Mean crown radius** (m)	**Trunk circum. breast ht.** (cm)	**Stump diameter** (cm)	**Sapwood rings** (no.)	**Dry leaf mass** (g)
1	7.4	3.0	1.1	202	85	N/A	3,750
2	6.7	2.6	2.0	77	30	112	9,750
3	4.7	1.5	1.1	45	29	89	2,210
4	7.8	1.5	1.4	57	22	97	5,230
5	7.5	3.0	1.8	75	30	130	6,790
6	5.9	1.4	1.2	37	14	70	1,950
7	7.2	1.6	1.1	57	22	113	4,420
8	6.7	1.7	1.5	60	23	103	5,380
9	9.9	2.4	3.6	132	49	172	29,300
10	4.2	1.4	1.1	38	25	86	1,830
11	6.8	2.3	1.5	59	22	76	5,230
12	6.3	1.7	1.2	42	17	72	2,200
13	7.5	2.0	1.8	68	29	95	9,040
14	4.4	2.4	2.1	53	21	86	5,930

Leaf areas of individual trees were also calculated by Equation 1 *(table 2):*

$$LA = LM * SLA \qquad \text{(Eq. 1)}$$

where LM was whole-tree leafmass (g) and SLA had a value of 6.03×10^{-3} m^2 g^{-1} obtained from the oak leaf sample. The LA for these trees ranged from 11.1-177 m^2, with a mean value of 40.0 m^2. LAI values for individual trees are shown based on LA and the area of crown projection for each tree modeled as a circle *(table 2).* (LAI was also calculated using measurements of crown radii and the equation for the area of an ellipse to find the area of crown projection, but the resulting values for LAI for each tree differed by only about one percent from those where crown radii were averaged.) The mean per-tree value for LAI was 4.4 m^2 m^{-2}.

Table 2—*Calculated values for tree parameters for native blue oak trees based on crown measurements, whole-tree harvest, and measurement of leafmass and SLA of a 50-leaf sample.*

Tree (no.)	**Crown depth** (m)	**Crown projection** (m^2)	**DBH** (cm)	**LMD** ($g\ m^{-2}$)	**Leaf area** (m^2)	**LAI** ($m^2\ m^{-2}$)
1	4.4	3.6	64	980	21.5	5.9
2	4.1	13	25	780	58.8	4.7
3	3.2	3.6	14	610	13.3	3.7
4	6.3	5.7	18	910	31.5	5.5
5	4.5	10	24	650	40.9	3.9
6	4.5	4.7	12	410	11.8	2.5
7	5.6	3.5	18	1,300	26.6	7.7
8	5.0	6.8	19	790	32.4	4.8
9	7.5	40	42	740	177	4.5
10	2.8	4.0	12	460	11.1	2.8
11	4.5	7.3	19	720	31.5	4.3
12	4.6	4.5	13	490	13.3	2.9
13	5.5	9.6	22	940	54.5	5.7
14	2.0	14	17	440	35.7	2.6

The sum of LA for all 14 trees was 560 m^2. The sum of areas of crown projection for the oak trees was 130 m^2, although overlap of foliage occurred. LAI calculated on the basis of the sum of LA area divided by the sum of areas of crown projection was 4.3 $m^2\ m^{-2}$, with crown projection taken as a circle with mean radius as noted in Table 1. LAI calculated on the basis of total leaf area divided by grid area was 1.8 $m^2\ m^{-2}$, and this value was considered to be the site LAI. This value was appropriate for the grove only; inclusion of surrounding area devoid of trees would result in an overall LAI value of perhaps half, or 0.9 $m^2\ m^{-2}$. Values ($m^2\ m^{-2}$) for LAI for oaks have been reported, including a range of 4.5-8 for a mixed oak forest in Castelporziano, Italy, and 4-6.75 for individual oak species at that Mediterranean site.

A Volumetric Method for Leaf Mass Estimation

A volumetric approach for estimating leaf mass has been used in past studies (Karlik and Winer 1999, Karlik and Winer 2001b, Miller and Winer 1984) because of its relatively simple non-destructive data requirements in field surveys, its potential applicability to the plethora of species found in natural landscapes, and its flexibility in modeling both tree and shrub morphology. Using crown height and radius data for each tree crown, volumes for five geometric solids approximating tree shapes (Karlik and Winer 1999, McPherson and Rowntree 1988) were calculated from the following geometric formulae: $4/3\pi r^3$ (sphere), $\pi r^2 h$ (cylinder), $2/3\pi r^2 h$ (vertical ellipsoid), $1/2\pi r^2 h$ (paraboloid) and $1/3\pi r^2 h$ (cone). These solids are related mathematically and the volumes of a vertical ellipsoid, paraboloid, and cone are respectively 2/3, 1/2 and 1/3 of the volume of a cylinder with the same radius and height. Calculated whole-tree leafmasses were obtained by multiplying the respective volumes by a leaf mass constant ($g\ m^{-3}$). A value of 280 $g\ m^{-3}$ was used for the leaf mass constant, the mean to two significant figures for coast live oak (*Quercus agrifolia)* (Miller and Winer 1984) and interior live oak (*Q. wislizenii)* (Horie and others 1991).

Total measured leaf mass for trees in this study of 92.9 kg may be compared to estimates of total leaf mass derived from the geometric solids, which ranged from 63.4 kg (cone) to 190 kg (cylinder). For the paraboloid, vertical ellipsoid and sphere, total leaf mass estimates were factors of 1.02, 1.36 and 1.15 of the measured, respectively. Therefore, two of the solids gave estimates of total leaf mass within 15 percent of the measured, and the third within approximately 35 percent. As a comparison, for 21 urban trees in the 1999 study of Karlik and Winer (1999), sums of leafmass estimates were within fractions of 0.91, 0.68, or 0.92 of the total measured leafmass when the vertical ellipsoid, paraboloid, or sphere solids were used, respectively. In the present study, the leaf mass constant of 280 g m^{-3} coupled with the paraboloid solid gave the closest estimate to measured leaf mass for the blue oak trees.

As a tree grows the ratio of leaf mass to volume will tend to decrease, because the outer surface of the crown moves up and out as branches grow, and crown volume increases as the cube of the distance from the center of the tree to the outer leaves. However, for small to medium sized trees (< 20 m in height), a leaf mass estimation method based on crown volume may work well in field surveys.

Allometric Relationships for LM

Allometric relationships for leafmass estimation were also obtained by plotting leafmass against crown and trunk dimensions, and also by plotting leafmass against calculated values such as area of crown projection. A second-order polynomial correlation of leafmass vs. circumference at breast height had a coefficient of determination (r^2) of 0.98 *(fig. 1).* A second-order equation was chosen rather than a linear relationship, because the leaf-carrying capacity of a plant is dependent upon vascular transport of water, and the area of the vascular system increases as the cross-sectional area of the stem, proportional to the square of the circumference or diameter. Circumference at breast height is perhaps the easiest tree dimension to measure, so the high value for r^2 is encouraging, and suggests oak circumference may be useful for estimating leaf masses for blue oaks. As expected, the graph of the second-order polynomial correlation for leaf mass vs. trunk DBH was identical in shape to that of leaf mass vs circumference, with the same r^2.

A second-order polynomial equation was also chosen to describe the correlation of leaf mass vs. mean crown radius because leaf mass should increase as the square of the crown radius, and for this correlation an r^2 of 0.96 was obtained *(fig. 2).* Leaf mass vs. area of crown projection modeled with a linear relationship resulted in an r^2 of 0.95. Therefore, leaf mass and either trunk or crown radius measurements appeared to be well-correlated for the trees studied. A second order polynomial correlation for leaf mass vs. stump diameter resulted in an r^2 of 0.92, almost as high as that for trunk DBH.

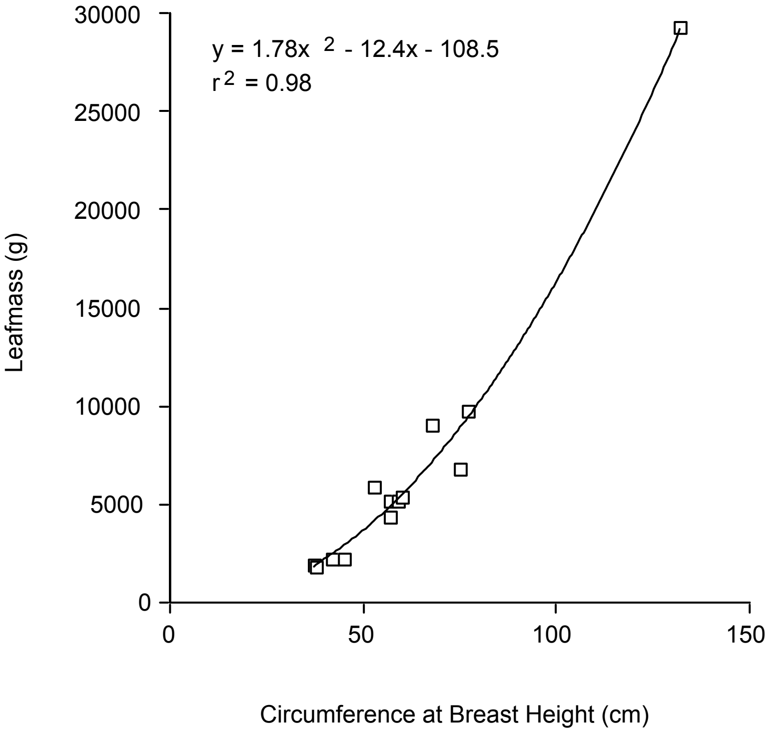

Figure 1—Allometric relationship between measured whole-tree leaf mass and trunk diameter at breast height for 14 blue oak trees harvested from a native stand in the Sierra Nevada foothills.

Several other relationships had lower coefficients of determination than those noted above. The linear relationship of leaf mass vs. rings of sapwood had an r^2 of 0.74, but for leaf mass vs. tree height or crown height r^2 had values of 0.55 and 0.39, respectively.

We are aware that only 14 blue oak trees were harvested in this study, and these trees were limited in ranges of trunk and crown dimensions. Therefore, the specific equations developed may not apply to trees outside this size range or to other species, and should be used with caution even for other blue oaks which fall within the size parameters of the harvested trees.

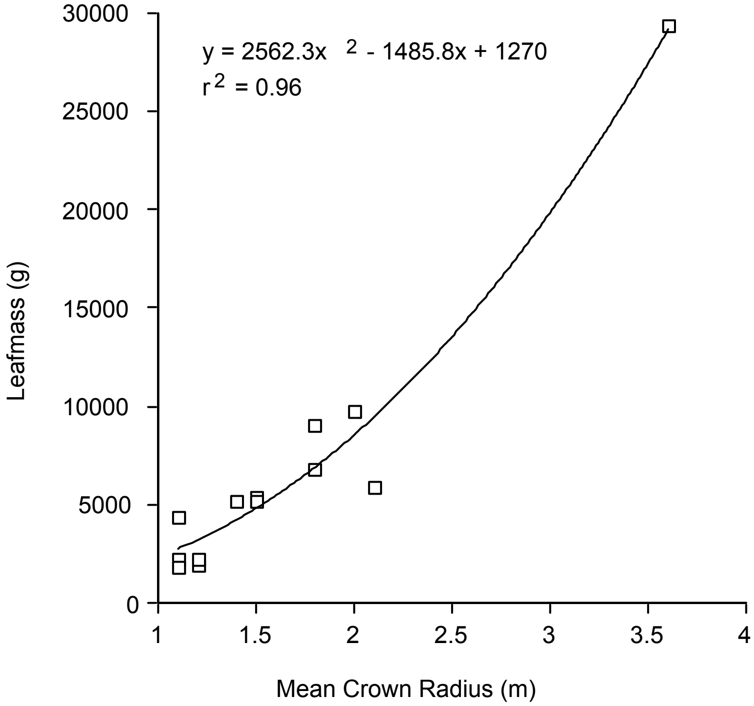

Figure 2—Allometric relationship between measured whole-tree leaf mass and mean crown radius for 14 blue oak trees harvested from a native stand in the Sierra Nevada foothills.

Implications for BVOC Emissions

Blue oaks fall within the Lepidobalanus subgenus of *Quercus*, a group characterized by high isoprene emissions but low or negligible monoterpene emissions (Csiky and Seufert 1999). An estimate of BVOC emissions under standard conditions of light and temperature (30°C and 1,000 µmol m^{-2} s^{-1} for photosynthetically active radiation) was calculated for the study site. (Hourly values for light and temperature and a canopy correction term would be used in a BVOC emission model.) Using a measured branch-level isoprene emission rate for blue oak of 27 µg g^{-1} h^{-1} (Karlik and Winer 2001a) and a value of zero for monoterpene emission rate based on taxonomy (Benjamin and others 1996), the estimate for isoprene flux would be 8.3 mg m^{-2} h^{-1}, equivalent to 7.7 mg C m^{-2} h^{-1}, which could also represent total BVOC emissions from the site since blue oaks are not monoterpene emitters. If we consider the oak stand to comprise 50 percent of the land surface in the vicinity, the emissions would be half, or 3.9 mg C m^{-2} h^{-1}. These values may be compared to estimates of 2.2-11 mg C m^{-2} h^{-1} for mixed deciduous/coniferous woodlands, and 0.8-4.3 mg C m^{-2} h^{-1} for scrub woodlands (Guenther and others 1994). The isoprene flux estimate derived for the stand of blue oaks investigated is at the higher end of the range for mixed deciduous/conifer woodlands, not unexpected considering the high isoprene emission rate for blue oak. The overall value of 3.9 mg C m^{-2} h^{-1} is at the higher end of the range for scrub woodlands. For California oak savannas, estimates of BVOC emissions such as these should be checked against fluxes measured at similar sites.

Conclusions

The LMD for the oak site we studied was calculated as the total leafmass divided by area of the grid needed to encompass the tree crowns. The resulting value of 310 g m^{-2} was considered to be the site LMD value, and may be compared to values for oak woodlands of various locales, and is about 80 percent of LMD values for U.S. woodland sites. However, the oak grove we harvested and measured was surrounded by open grassland, and therefore an LMD value of 310 g m^{-2} represented a maximum for that landcover. If the oak LMD was calculated on the basis of the area of the grove plus the open grassland surrounding it, the value would have no more than half, and the resulting value of approximately 150 g m^{-2} is less than 50% of the value for eastern deciduous forests, but close a reported value for oaks at an Italian site.

The mean value for LAI for the 14 individual trees in this oak site was 4.4 m^2 m^{-2}. LAI calculated on the basis of total leaf area divided by grid area was 1.8 m^2 m^{-2}, and this latter value was considered to be applicable to the site. This value was appropriate for the oak grove only; consideration of the surrounding area which was devoid of trees would result in an overall LAI value of less than 0.9 m^2 m^{-2}, which is lower than reference values for a Mediterranean oak woodland.

For estimating leaf mass, both a volumetric method and an allometric method based on tree dimensions worked well. Modeling tree crowns with a paraboloid gave calculated leaf mass within 2 percent of the total measured leaf mass for these trees. The relationship between leafmass and circumference at breast height had the highest coefficient of determination of the relationships studied, suggesting trunk circumference may be used to estimate leaf masses for blue oaks. Mean crown radius and crown projection were also well-correlated with leaf mass. A volumetric method may be useful in future field studies for leaf mass estimation.

BVOC estimates indicate blue oaks may be significant contributors of isoprene to California airsheds where this species is plentiful. BVOC fluxes should be measured for oak savannas for comparison to estimates.

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Phytophthora ramorum and Sudden Oak Death in California: I. Host Relationships[1]

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Abstract

A new canker disease of *Lithocarpus densiflorus*, *Quercus agrifolia*, *Q. kellogii*, and *Q. parvula* var. *shrevei* in California is shown to be caused by *Phytophthora ramorum*. The pathogen is a recently described species that was previously known only from Germany and The Netherlands on *Rhododendron* and *Viburnum*. This disease has reached epidemic proportions in mixed evergreen and redwood forests over an area approximately 300 km long along the central coast of California. The most consistent and diagnostic symptoms on larger trees are the cankers that develop before foliage symptoms become evident. Cankers have brown or black discolored bark, seep dark red sap and occur on the trunk at the root crown up to 20 m above the ground. Cankers do not enlarge below the soil line into the roots. Cankers can be over 2 m in length and are delimited by thin black zone lines in the inner bark. Foliage on affected trees often turns from a healthy green color to brown over a period of several weeks. In *L. densiflorus* saplings, *P. ramorum* was isolated from branches as small as 5 mm diameter. *Lithocarpus densiflorus* and *Q. agrifolia* inoculated with *P. ramorum* in the field and greenhouse developed symptoms similar to those of natural infections. The pathogen was re-isolated from inoculated plants, thereby confirming pathogenicity. Based on field observations and greenhouse inoculations, the host range of *P. ramorum* in California has been expanded and now includes *Rhododendron* spp., madrone (*Arbutus menziesii*), huckleberry (*Vaccinium ovatum*), manzanita (*Arctostaphylos* spp.), California bay laurel (*Umbellularia californica*), buckeye (*Aesculus californica*), bigleaf maple (*Acer macrophyllum*), toyon (*Heteromeles arbutifolia*), California coffeeberry (*Rhamnus californica*), and California honeysuckle (*Lonicera hispidula*). On these hosts, *P. ramorum* causes a variety of foliar and branch symptoms.

Introduction

Over the past 7 years, a disease of tanoak (*Lithocarpus densiflorus*), coast live oak (*Quercus agrifolia*) and California black oak (*Q. kelloggii*) has caused considerable mortality in central California (Garbelotto and others 2001, McPherson and others 2000). Named "Sudden Oak Death" in the popular press, the whole crown

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of affected trees often appears to die rapidly, and the foliage may turn from an apparently healthy green to brown within a few weeks. The most consistent and diagnostic symptom of the disease on larger trees is the development of cankers that have brown or black discolored bark on the lower trunk and seep dark red sap. The cankers do not extend into the roots. These cankers develop before foliage symptoms become evident. Such discoloration and bleeding are common symptoms associated with infection by *Phytophthora* species on oaks (Brasier and others 1993, Mircetich and others 1977, Tainter and others 2000). In agreement with this observation, we have consistently isolated the recently described *Phytophthora ramorum* from diseased *L. densiflorus* and *Quercus* spp. (Rizzo and others [In press]). The current range of the pathogen is considered to be from Big Sur in Monterey County to southern Oregon; the furthest inland sites are in western Solano County (Kelly 2002). Previously, *P. ramorum* had only been reported on ornamental rhododendron and viburnum in Germany and the Netherlands (Werres and others 2001). Field and greenhouse inoculations of tanoak and coast live oak seedlings, saplings, and mature trees produced symptoms similar to those observed with natural infections and confirmed the pathogenicity of *P. ramorum* (Rizzo and others [In press]).

To date, most work on this disease in California has concentrated on oaks. However, the finding of *P. ramorum* on rhododendron in Europe suggested that the host range of the pathogen in California needed further investigation. To understand the potential impact on oak trees we must have a thorough understanding of the biology of this pathogen including the complete host range, transmission dynamics and population biology of the pathogen. In this paper, we describe our efforts to determine the host range of *P. ramorum* in California including field isolations and inoculations of non-oak hosts. We also report on inoculations of two California white oak species from which the pathogen has not been found in the field, valley oak (*Q. lobata*) and blue oak (*Q. douglasii*). Two red oak species from eastern North American, northern red oak (*Quercus rubra*) and pin oak (*Quercus palustris*), were also included in these inoculations. In parts II (Davidson and others 2002) and III (Garbelotto and others 2002), we describe preliminary results on the transmission mechanisms and genetics of the pathogen, respectively. Finally, in part IV (Garbelotto and others 2002), we discuss initial results from chemical control studies of *P. ramorum*.

Methods

Field Survey

Symptomatic and dead trees and shrubs were examined throughout the known range of *P. ramorum*. At each site, samples were taken from trees that matched symptoms of *Phytophthora* infection and returned to the laboratory for isolation. Specific locations of sampled hosts were marked using global positioning equipment (GPS, Trimble Corp., Sunnyvale, California) and entered into a monitoring database maintained by Dr. Maggi Kelly, University of California, Berkeley (http://camfer.cnr.berkeley.edu/oaks/). Additional data collected with each sample included host species, host symptoms, tree diameter, forest type, overall stand health, and relationship to other symptomatic trees. Where possible, samples were collected from multiple hosts at each location.

Isolation methods for *P. ramorum* on oaks are described elsewhere (Rizzo and others [In press]). For hosts with foliar lesions, discolored and necrotic areas were excised from leaves and placed in petri dishes (either in the laboratory or in the field) containing pimaricin-ampicillin-rifampicin-PCNB agar (PARP), a selective medium for *Phytophthora* species (Erwin and Ribeiro 1996). Plates were incubated in the dark at 20 to 22°C and examined within 2 to 5 days. We have also developed PCR (polymerase chain reaction) primers based on the nucleotide sequences of the internal transcribed spacer (ITS) region of the nuclear ribosomal DNA that are specific for *P. ramorum* (Garbelotto and others 2002). We have used these primers to successfully amplify DNA from infected leaves of multiple hosts and have used this methodology to pre-screen most foliar hosts (Garbelotto and others 2002).

Inoculation Trials

Greenhouse trials were conducted on seedlings of potential host species to evaluate the pathogenicity of *P. ramorum*. Inoculum was prepared by growing isolates on V-8 juice agar for 7 days, then cutting out 5 mm diameter plugs using a sterilized cork borer. Three isolates of *P. ramorum* were used for all tests: Pr-5 from tanoak, Pr-6 from coast live oak, and Pr-52 from rhododendron. Methods for stem inoculations of oak seedlings are described elsewhere (Rizzo and others [In press]). Foliar hosts were selected based on results of positive field isolations; a complete range of all woody plants found in oak forests have not been tested. Plants were purchased from native plant nurseries and were typically 2-3 years old. Foliage inoculations were conducted by misting leaves with sterile distilled water (SDW) and then pinning inoculum plugs to the upper surface of leaves. Sterile agar plugs were used as controls. A zip-loc plastic bag was then placed over the individual leaves; prior to sealing the bag the leaves were misted again with SDW. Each trial consisted of 10 leaves per host species per isolate plus controls. For most trials, the three isolates of *P. ramorum* listed above were used. On each of five seedlings, two leaves per isolate plus two control leaves were inoculated. Seedlings were incubated for 2 weeks in a greenhouse that was maintained at 22 to 24°C. For each trial, symptoms were recorded, lesion length and width was measured and pieces of stems or leaves were plated on PARP to verify presence or absence of *P. ramorum*. All leaf inoculations were conducted twice.

Results

Field Isolations

We have recovered *P. ramorum* via isolation and direct PCR from symptomatic plant tissue of the following tree species: madrone (*Arbutus menziesii*), California bay laurel (*Umbellularia californica*), buckeye (*Aesculus californica*), huckleberry (*Vaccinium ovatum*) and *Rhododendron* spp. (cultivars “Gomer Waterer” and “Colonel Coen,” *R. macrophyllum*) *(table 1).* Using the direct PCR method on symptomatic leaf tissue, we have also detected *P. ramorum* DNA from field samples of manzanita (*Arctostaphylos manzanita*), bigleaf maple (*Acer macrophyllum*), toyon (*Heteromeles arbutifolia*), California coffeeberry (*Rhamnus californica*), and California honeysuckle (*Lonicera hispidula*). However, at the present time, we have been unable to isolate *P. ramorum* from these latter hosts. In all cases, *P. ramorum* was recovered from aboveground plant parts such as leaves or branches *(table 1).* Of the non-oak hosts, madrone, manzanita, rhododendron, and huckleberry appear to show the most dieback associated with the disease in the field.

Table 1—Known hosts of *Phytophthora ramorum* in California and their method of detection in the field.

Host[1]	Common name	Plant part infected	Method of detection[2]	
			Field isolation	Direct PCR
Quercus agrifolia (Fagaceae)	Coast live oak	main stem	+	+
Q. kellogii (Fagaceae)	California black oak	main stem	+	+
Q. parvula var. *shrevei* (Fagaceae)	Shreve's oak	main stem	+	nt
Lithocarpus densiflorus (Fagaceae)	Tanoak	main stem, branches, leaves	+	+
Umbellaria californica (Lauraceae)	Bay laurel	leaves	+	+
Arbutus menziesii (Ericaceae)	Madrone	branches, leaves	+	+
Vaccinium ovatum (Ericaceae)	Huckleberry	main stem, branches, leaves	+	+
Arctostaphylos spp. (Ericaceae)	Manzanita	branches, leaves	-	+
Rhododendron spp. (Ericaceae)	Rhododendron	branches, leaves	+	+
Aesculus californica (Hippocastanaceae)	Buckeye	branches, leaves	+	+
Acer macrophyllum (Aceraceae)	Big leaf maple	leaves	-	+
Heteromeles arbutifolia (Rosaceae)	Toyon	branches, leaves	-	+
Rhamnus californica (Rhamnaceae)	California coffeeberry	leaves	-	+
Lonicera hispidula (Caprifoliaceae)	California honeysuckle	leaves	-	+

[1] *Rhododendron* spp. and *Viburnum* sp. have been found as hosts of *P. ramorum* in The Netherlands and Germany.

[2] Symbols: +, positive isolation or detection by PCR; -, tested but not recovered with this method to date; nt, not tested.

Seedling Inoculation Trials

In all hosts tested, *P. ramorum* was reisolated after two weeks from inoculated leaves and not from control leaves *(table 2).* With the two *Quercus* species, lesions were no larger than a typical control wound after 2 weeks (mean width, 1.9 mm), however *P. ramorum* was still reisolated. Mean lesion width on bay and toyon was only slightly larger than found on oak (mean lesion width, 5 mm). Lesions on huckleberry, manzanita, and tanoak often covered the entire inoculated leaf and in some cases, the pathogen grew through the petioles to colonize branches and stems. With madrone and bigleaf maple, lesions were often over 4 cm in diameter.

Table 2—*Pathogenicity of* Phytophthora ramorum *on leaves of selected native California plant species.*

	Disease rating[1]	
Host	***P. ramorum***	**Control**
Quercus agrifolia	+	-
Q. kellogii	+	-
Lithocarpus densiflorus	+++	-
Umbellaria californica	++	-
Arbutus menziesii	+++	-
Vaccinium ovatum	+++	-
Arctostaphylos manzanita	+++	-
Rhododendron macrophyllum	+++	-
Aesculus californica	++	-
Acer macrophyllum	+++	-
Heteromeles arbutifolia	++	-

[1] Plants were evaluated after 2 weeks using the following disease rating scale: -, < 5 mm lesion around pin, *P. ramorum* not isolated; +, < 5 mm lesion around pin, *P. ramorum* isolated; ++, 5 mm to 20 mm leaf spots, *P. ramorum* isolated; +++, > 20 mm leafspots; often entire leaf colonized or discolored, *P. ramorum* isolated.

In the oak seedling trial, *P. ramorum* caused lesions that were significantly greater than found on the controls in each of the red oak species and tanoak, but not in the two white oak species (ANOVA, $P < 0.05$) *(table 3).* In the seedlings inoculated with *P. ramorum*, the external surface of the bark was sunken along the entire length of colonization by the pathogen. Internal discoloration was generally limited to the phloem although some xylem discoloration was apparent. *Phytophthora* was recovered from all inoculated stems, including valley oak and blue oak, and none of the controls. The results of the inoculations of tanoak and coast live oak in this study are consistent with those reported in a previous experiment (Rizzo and others [In press]).

Table 3—*Mean and range in lesion length in tanoak, red oak and white oak seedlings resulting from inoculations with Phytophthora ramorum.*

	Mean length of discoloration, cm[1] (range of discoloration)	
Host	***P. ramorum*** **N=30**	**Control N=10**
Lithocarpus densiflorus	4.7 (1.7 – 21.0)	1.5 (0.9 – 4.0)
Quercus agrifolia (red oak group)	2.3 (1.3 – 4.8)	1.0 (0.7 – 1.4)
Quercus kellogii (red oak group)	3.1 (1.5 – 8.0)	1.3 (1.1 – 1.5)
Quercus rubra (red oak group)	4.4 (1.2 – 9.7)	1.4 (1.0 –2.0)
Quercus palustris (red oak group)	3.3 (0.7 – 8.1)	1.3 (1.1 – 1.5)
Quercus douglasii (white oak group)	1.3 (0.7 – 2.4)	0.8 (0.3 – 1.3)
Quercus lobata (white oak group)	1.4 (0.8 – 2.2)	1.0 (0.6 – 1.6)

[1] Thirty seedlings of each host species were inoculated with three isolates of *P. ramorum* (10 seedlings per isolate). Data for all three isolates are combined in the table. *Phytophthora ramorum* was recovered from all inoculations including *Q. douglasii* and *Q. lobata*; *P. ramorum* was not recovered from the control inoculations. Based on ANOVA, lesion lengths were significantly different between *P. ramorum*-inoculated seedlings and controls except for *Q. douglasii* and *Q. lobata*.

Discussion

These data clearly indicate that *P. ramorum* infects many different plant species in addition to oaks and tanoak in coastal California forests. In some mixed-evergreen forests nearly all woody plants can serve as host for *P. ramorum*. For example, at China Camp State Park in Marin County, the overstory consists of coast live oak, black oak, bay laurel, and madrone. Toyon is the primary understory shrub species. Buckeye and manzanita are found at the margins of closed canopy. Valley oak (in riparian areas and at the edge of the closed canopy) appears to be the only woody plant species unaffected by *P. ramorum* at this location. There are many other plant species that co-occur with oaks and tanoak that have not been tested for susceptibility to *P. ramorum*. This includes additional species in the Ericaceae (e.g., salal). Species in this family appear to be the most affected after the oaks. As the geographic range of *P. ramorum* changes, it will potentially encounter other hosts that are not found in forests in the current range.

Exotic species of *Phytophthora* have been considered responsible for extensive tree mortality and negative ecological impact in forests of Australia, Europe and

North America (Brasier 2000, Hansen 2000, Old and Dudzinski 2000). *Phytophthora cinnamomi* has devastated the jarrah forests of western Australia, killing over 50 percent of all plant species over several hundred thousand hectares (Weste and Marks 1983). The broad host range of *P. ramorum* that we have discovered in California forests suggest that this pathogen has the potential to cause similar, long-term landscape level changes in these forests. Loss of oaks and other overstory trees and shrubs will have cascading effects on these ecosystems including increased fire hazards, soil erosion, and loss of habitat for wildlife (McPherson and others 2000, Garbelotto and others 2001). Developing restoration plans for these ecosystems will represent a significant future challenge for forest managers.

The most encouraging result from our inoculation study was the finding that *P. ramorum* did not cause lesions on valley oak and blue oak that differed significantly from the control wounds. However, the pathogen did survive in the discolored tissue for at least 6 weeks following inoculation. It is unknown if the pathogen can continue to survive for long periods in white oak tissue and eventually cause mortality of plants. To date, no species in the white oak group has been diagnosed with the disease in the field. Further studies in the greenhouse are planned.

We report our initial results of a study comparing the susceptibility of California oaks and eastern North American oak species to *P. ramorum*. Challenging seedlings of northern red oak (*Quercus rubra*) and pin oak (*Quercus palustris*) with *P. ramorum* resulted in longer lesions in the bark than those that developed in the coast live oak and California black oak. Lesions in northern red oak were nearly twice as long as those observed in coast live oak and about the same length as those observed in tanoak. Tanoak is considered to be the most susceptible California tree species to *P. ramorum*. Extrapolation of results from seedling experiments to the potential effects on mature trees must be done cautiously. However, because lesion sizes in red oak and pin oak seedlings were much larger than in coast live oak seedlings (a species in which the adults are very susceptible), we suggest that it is likely that mature trees of northern red oak and pin oak will be susceptible to infection by *P. ramorum*. Therefore, efforts to prevent spread of *P. ramorum* to eastern North American forests are critical.

An understanding of the host range and spatial distribution of the pathogen is pivotal in formulating hypotheses for further epidemiological research (e.g. Davidson and others 2002), developing monitoring strategies and management guidelines that may either prevent further spread of the disease or ameliorate disease conditions where the disease may be only recently present.

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Phytophthora ramorum and Sudden Oak Death in California: II. Transmission and Survival[1]

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Abstract

The newly discovered *Phytophthora ramorum* canker disease of oak (Sudden Oak Death Syndrome) threatens millions of acres of California woodlands where coast live oak (*Quercus agrifolia*), tanoak (*Lithocarpus densiflorus*), or black oak (*Quercus kelloggii*) are dominant species. An important step in controlling this disease involves understanding how it is spread. The presence of diseased oaks at all elevations on hillsides and the above-ground nature of the disease suggest wind-blown rain or rain splash as a common mechanism for movement of spores. Although viable spores have yet to be found on infected oak tissue, other hosts may serve as sources of rain-dispersed inoculum. In the laboratory, abundant sporangia form on moistened leaves of infected bay (*Umbellularia californica*) and *Rhododendron* spp. within 72 hours. These sporangia break off and easily disperse in water. Chlamydospores were also observed on the surface of moistened bay leaves. Consistent with these results, *P. ramorum* has been recovered from rain, soil, litter, and stream water from woodlands with infected oak and bay trees. Spores of *P. ramorum* do not survive drying, but in moist conditions can survive for at least one month.

Introduction

The newly described *Phytophthora ramorum* canker disease of oak (Sudden Oak Death Syndrome) threatens millions of acres of California woodlands where coast live oak (*Quercus agrifolia*), tanoak (*Lithocarpus densiflorus*), or black oak (*Quercus kelloggii*) are dominant species (Garbelotto and others 2001, McPherson and others 2000). An important step in controlling this disease involves understanding how it is spread, both on a small scale between oak trees in an infected area, and over a larger scale from infected to uninfected woodlands. Transmission consists of spore production, movement of spores, and infection of a new individual. Knowledge of the necessary conditions for each of these steps may help us establish barriers to the

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spread of infection within a single park or between geographically separated host plant ranges such as the Coastal mountains and the Sierra Nevada of California.

Phytophthora species generally reproduce through both dormant (resting) spores, as well as rapidly produced fruiting bodies (sporangia) that contain swimming spores (zoospores). Dormant spores may either be sexual (oospores) or asexual (chlamydospores) (Erwin and Ribeiro 1996). The production of sporangia generally requires very high humidity, and therefore, will be strongly affected by seasonal temperatures and rainfall (Duniway 1983). Survival of all spore types will also be affected by temperature and moisture (Duniway 1983). In addition, production and viability of spores may differ on each host species.

Once produced on or within the host plant, spores may spread via rain, soil, stream water, or movement of the infected plant itself. Movement of plant material may include infected nursery stock, firewood, or timber. Transport of soil containing propagules may occur on shoes of hikers, tires of trucks and mountain bikes, or the feet of animals. Movement of spores in stream water may allow for long-distance transport, depending on viability of spores in water, and the potential of spores to move from stream water to the susceptible parts of host plants (Hansen and others 2000). Rain splash has been shown to move *Phytophthora* spores of other species over several meters (Ristaino and Gumpertz 2000), making this a potentially effective means of local transport, especially for spores requiring moisture for production and survival.

The mode of transmission for *P. ramorum* among California oaks is complicated by the presence of many other host plant species in the forest. Currently, the host list includes 10 non-oak plant species in five plant families (Rizzo and others 2002). These other hosts may serves as sources of inoculum and act as infectious links among oak trees. In addition, nursery stock of host plant species, such as rhododendron, can serve as vectors of disease when moved for landscaping.

In this paper, we provide data on the types of spores produced by *P. ramorum* under laboratory and natural host plant conditions. We also document the seasonality of spore production in recovery from rainwater, soil, and stream water. Finally, we use survival of zoospores and chlamydospores in the laboratory in water, and on dry and moist filter paper to simulate viability of spores in stream water, and under moisture extremes on solid substrates, such as litter or soil.

Methods

Production of Spores

A total of 119 isolates of *P. ramorum* were obtained from six host species (coast live oak, black oak, shreve oak (*Quercus parvula* var. *shrevei*), tanoak, bay, and ornamental rhododendron spp.) in 36 locations over an area approximately 300 km long from Monterey to Mendocino County, and ranging up to 65 km inland (Rizzo and others, in press). These isolates were grown on pimaricin-ampicillin-rifampicin-PCNB agar (PARP) and Corn Meal Agar (CMA) in the laboratory and examined for spore production. They were also cultured on V8 medium and V8 agar plugs were put in soil water extract at 18-23 °C for 24 hours to examine sporangia production. (For methods, see Rizzo and others, in press.)

Production of spores were also monitored on pieces of naturally infected host tissue collected from forest and nursery sites within the 300 km host range. Eight excised coast live oak cankers, 9 infected bay leaves, and 15 infected nursery rhododendron leaves were placed in moist chambers at 18-23 °C for 72 hours and monitored for spore production. In addition, the bleeding sap was collected when possible from 13 coast live oak at weekly intervals from April 22 to July 16, 2001, and plated on PARP medium to test for the presence of viable pathogens.

Movement of Spores

During the isolation of *P. ramorum* from 93 oak and tanoak trees, field observations of the position of cankers on trees and the location of infected trees with respect to topography were used to gain insight into the mechanisms of spore movement, whether above ground, moved in soil, or carried by rain runoff or streams. Location of infection on 20 bay trees and 6 rhododendron bushes also was noted. Recovery of spores was attempted from rainwater, soil, litter, and stream water in a time series spanning the winter rains and the drying summer months.

Rainwater

Raintraps were used to collect rainwater in a coast live oak woodland at Fairfield Osborn Preserve in Sonoma Co. Both coast live oak and bay trees were infected with *P. ramorum* at this site. Raintraps consisted of a 165 cm by 75 cm vinyl sheet stretched over a pvc frame and folded into a funnel with a 4 liter collecting jar at the bottom. Traps were set up on February 2, 2001 and used to collect rainfall through winter, and for one unusually late rain on June 27-28. Two traps were placed 0.5 m in front of cankers on each of 7 oak trees, for a total of 14 traps. Previous isolations confirmed that the cankers were caused by *P. ramorum* infection. Two “distant” traps were placed at a distance of 5 m from all infected oak trees. Four additional “distant” traps were installed on March 15, 2001. Although separated from infected oaks, “distant” traps still were under the forest canopy, which consisted mainly of bay trees. Rain water was collected at approximately 2-day intervals during a storm event. Rainwater was stored overnight at 4-5 °C to allow spores to settle. One liter of water was suctioned off of the bottom of containers and filtered through a Millipore 3 µ cellulose esterase filter to capture all spore types. The filter was then cut into strips and placed filtrate side down on selective medium plates. After 7 days, strips were removed, and colonies of *P. ramorum* were counted.

Soil

Beginning in March, 2001, soil and litter were collected on a monthly basis from around the base of 15 diseased oak trees at the Fairfield Osborn Preserve to test for the presence of *P. ramorum.* Previous isolations confirmed that all trees were infected by *P. ramorum*. At the base of each tree on the infected side, soil was collected in zip-lock bags from three separate spots and pooled to equal 500 g. Litter was collected at three spots to fill one-fourth the volume of a gallon zip-lock bag. A green d’anjou pear was pressed into the soil or litter in each sample so that one-third of the pear was immersed, and diH20 was added to the sample until one-half of the pear was immersed in water. Samples were allowed to sit for 6 days at 18-23 °C. Pears were then removed, washed, and monitored for signs of *Phytophthora* lesions. Tissue from likely lesions was plated on PARP selective medium to verify *P. ramorum* presence.

Stream Water

Water was collected from Bean Creek, Santa Cruz Co., on a bi-monthly basis from April through June 2001 in a forested area with infected coast live oak and tanoak trees. Sampling ended in June because the stream dried up. For each sample, 8 liters of stream water were stored in plastic bins at 18-23 °C. Two d'anjou pears were added to each bin so that pears were halfway immersed in stream water. After 5 days, pears were removed and *P. ramorum* infection was assessed as for soil baiting (see above).

Survival of Spores

To assess survival of spores under various moisture regimes, suspensions of zoospores and chlamydospores of *P. ramorum* were each added to water, moist filter papers, or dry filter papers (Fisherbrand P4 4.25 cm) and monitored for viability for one month. The suspensions for both types of spores consisted of a pool of spores from fifteen isolates. Approximately 200 spores in 100 ul of suspension were added to either (1) 100 ul of diH20; (2) a filter moistened to saturation with 100 ul diH20; or (3) a dry filter. The moistened filters were kept in closed screw-cap tubes. An additional 150 ul dH20 was added to the moist filter at two week intervals to maintain saturation. The dry filters were allowed to dry completely at room temperature (23 °C, 30 percent rh, 30 minutes) and placed in a crisper. All treatments were stored at 15 °C. Five replicates of each treatment were plated on selective medium at 0, 3, 7, 15, and 30 days for chlamydospores, and 0, 7, 15, and 30 days for zoospores. Colonies were counted at 36 and 72 hours to assess viable spores.

Results

Production of Spores

In laboratory culture, all 119 isolates of *P. ramorum* produced large numbers of chlamydospores, the asexual resting spores. In addition, all isolates produced large numbers of sporangia within 24 hours when grown on V8 agar plugs in soil water. These sporangia were highly deciduous at 20 °C, meaning that they easily detached from the hyphae for dispersal. These detached sporangia were observed to either germinate directly or to release zoospores. Oospores, the sexual resting spores, were not observed on either medium for any of the 119 isolates.

Spore production was observed on tissue of some host species. Sporangia were present on the surface of 3 of 9 infected bay leaves and all 15 rhododendron leaves within 72 hours. Chlamydospores were also observed on the surface of one bay leaf. No spores were observed on the surface of oak bark cankers. Sporangia were observed microscopically in the bleeding sap of one oak tree. However, none of the 81 plating attempts of bleeding sap from the 13 trees resulted in colony formation.

Movement of Spores

Field Observations

Observations suggest that spores of *P. ramorum* were aerially dispersed. Of the 93 oak and tanoak trees from which *P. ramorum* was isolated, none had cankers below the root crown. Cankers on one tanoak were as high as 20 m. Of the six rhododendrons sampled, all infection was in the leaves or stems. Of 20 bays sampled, all successful isolation was from leaves, although lesions were present on some terminal twigs. Infections on oaks were observed from sea level to 800 m and at all elevational positions on hillsides ranging from valleys to ridgetops. Infection did not strictly follow water courses.

Raintraps

Rainwater contained viable spores of *P. ramorum (fig. 1)*. At some point during the sampling period, *P. ramorum* was recovered from rain captured in traps placed at all seven of the coast live oaks. This rainwater was a combination of throughfall rain, drip from the canopy, and splash from the trunk. Propagule counts were low, but present in rainwater from these traps at each of the collection periods except for the brief summer storm in late June (0.5 inches rainfall). Spore counts were variable from tree to tree, and ranged from 0.25-7 spores per liter in positive samples from traps placed at the oak trees. Of the six "distant" traps placed under the forest canopy but 5 m away from infected oak trees, two were positive for *P. ramorum* during the sampling period.

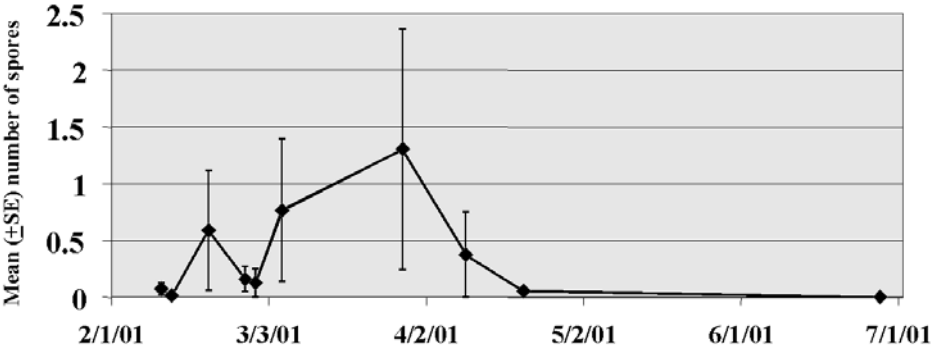

Figure 1—Mean number of *P. ramorum* spores per liter of rainwater (± standard error) for storms occurring from February through June, 2001 at the Fairfield Osborn Preserve, Sonoma Co. Means were based on the average from two collecting traps at each of seven coast live oak trees.

Soil Baiting

Soil and litter also contained viable propagules of *P. ramorum*. During March, 3 of 15 soil samples and 1 of 15 litter samples tested positive. During April, no soil samples tested positive, and only 1 of 15 litter samples tested positive. During May, no litter samples tested positive, and only 1 of 15 soil samples tested positive. The positive May sample was from the same tree as the positive April sample. In June and July, all samples were negative.

Stream Baiting

The April sample from Bean Creek was positive for *P. ramorum*. Samples from May and June were all negative.

Survival of Spores

A portion of both the zoospores and chlamydospores survived in the water and moist filter treatments *(fig. 2)*. Both types of spores were killed by the drying process at 30 percent rh at room temperature in the "dry filter" treatment (data not shown). Chlamydospores, thick-walled resting spores, survived better than zoospores in both the water and moist filter treatments. Zoospore survival averaged less than 20 percent at the end of the 30-day period while chlamydospore survival at 30 days in water and on moist filters still averaged 75 percent and 41 percent of starting values, respectively.

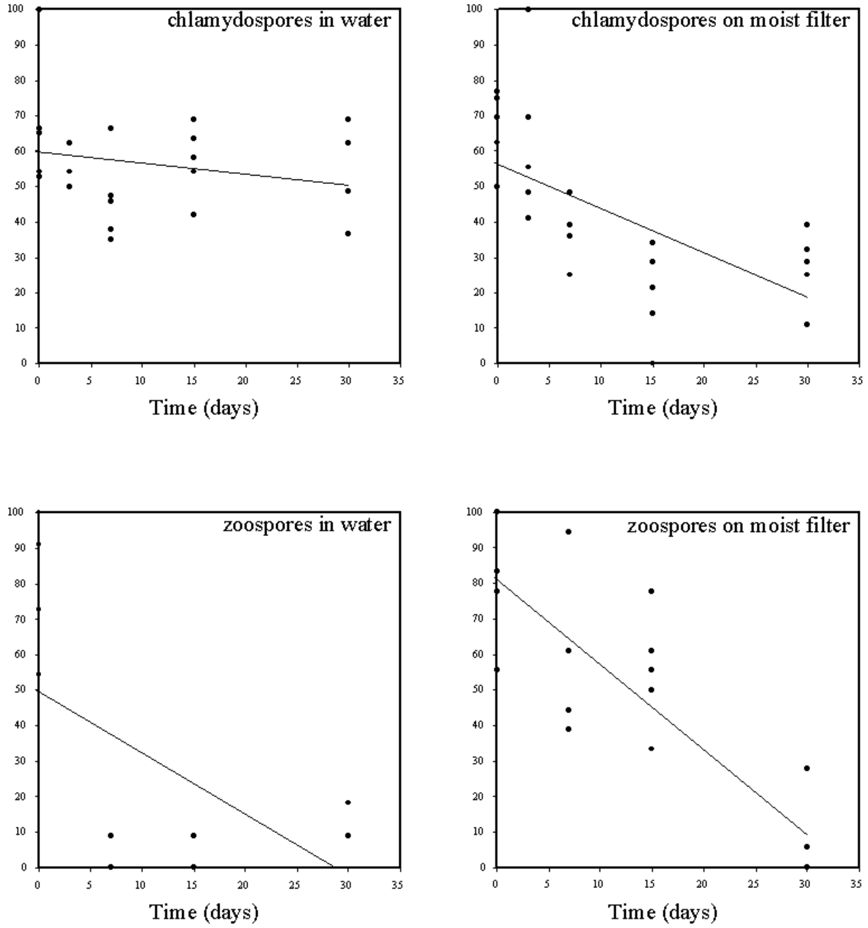

Figure 2—Survival over time of *P. ramorum* chlamydospores and zoospores in water and on moist filter paper at 15 °C. Each datum represents the viable spore count (scored by germination) for one of five treatment replicates plated to agar at a given time point. Spore count data is scaled as a percent of the highest spore count at time (0) to facilitate comparison among graphs.

Discussion

Current data suggest that *P. ramorum*, the causal agent of "sudden oak death," may have been introduced to northern California approximately a decade ago (Garbelotto and others 2001, Garbelotto and others 2002, McPherson and others 2000). Today, the range of the pathogen covers over 600 km, from Big Sur into southern Oregon. This rate of spread surpasses that of Chestnut Blight in the early part of the 20th century (Anagnostakis 1987). Our data on transmission and survival of *P. ramorum* provide preliminary insight into the mechanisms underlying this remarkable spread.

The rapid production of spores on foliar hosts, such as bay and rhododendron, may be key to the spread of *P. ramorum* within a locality, and perhaps between different geographic locations. *P. ramorum* produced sporangia on moistened leaves of both bay and rhododendron, the two foliar hosts tested. Chlamydospores were also noted on infected bay leaves. In addition, we have observed chlamydospores on infected rhododendron leaves in moist chambers for other experiments.

While rhododendrons are not major components of most California forests, bay trees are dominant species in many coast live oak forest types. Consistent with laboratory results on spore production, evidence from the field suggests that inoculum from bay trees may be very important in vectoring *P. ramorum* to oaks. Swiecki and Bernhardt (2001) found a significant association between infected oaks and the presence of bay trees. Rainwater traps in this study placed 5 m from infected oaks contained viable spores that may have come from overstory infected bay trees. Furthermore, we often observe an increase in *Phytophthora*-like leaf spots on bays growing within oak infection centers. To further investigate the importance of bay as an inoculum source, studies are underway to determine temperature requirements for sporangia production on bay leaves, the viability of *P. ramorum* in leaves attached to trees or fallen in litter, and the distance spores can travel from bay leaves.

The negative results of spore production on oak bark cankers or in bleeding sap require further investigation. Rapid contamination of oak cankers by fungal species may have prevented sporulation of *P. ramorum*. In addition, the seasonal state of the bark may not have been conducive to spore production at the time of the test (Brasier and Kirk 2001). However, successful amplification of *P. ramorum* DNA from bleeding sap (Garbelotto and others 2002), suggests the presence of propagules and underscores the need for additional isolation attempts from sap.

Viable spores of *P. ramorum* were shown to be carried in rainwater, soil, litter, and stream water. The presence of diseased oaks at all elevations on hillsides and the above-ground nature of the disease suggest wind-blown rain or rain splash as a common mechanism for movement of spores. The abundance of viable propagules exhibited a distinct seasonality, peaking in March and early April of 2001, a low rainfall year. Production of sporangia by other *Phytophthora* species depends on high moisture levels (Duniway 1983). Hence, the presence of moisture from rain on infected plant tissue is probably necessary for production of spores that eventually end up in soil, litter, or stream water. Generally increasing levels of inoculum in rainwater in early April, and the lack of spores in the isolated, 2-day June rain, may suggest that a time of prolonged moisture is needed for inoculum buildup. Warming temperatures in early April during the period of consistent rainfall may also have contributed to the peak in spore production. Failure to recover *P. ramorum* from soil and litter in the summer months may indicate that seasonal drying is sufficient to reduce viability of spores in these substrates.

Survival of *P. ramorum* spores also depended on moisture levels. In laboratory tests, both chlamydospores and zoospores placed in suspension on filter paper were killed by drying for one-half hour at 30 percent relative humidity. However, with moist conditions, zoospores and chlamydospores of *P. ramorum* can survive for at least a month, and this study suggests that chlamydospores probably survive much longer. Because moisture loss appears to be one way to kill spores of *P. ramorum*, we are initiating studies to determine survival times for spores under a range of humidity levels. Pairing laboratory data on moisture requirements for spore survival with climate data from forests may help us predict how long spores are present in litter and soil after rains cease, and hence, when closure of areas to the public or logging may be warranted.

Given the ability of *P. ramorum* to produce spores on foliar hosts which can then be carried in wind-blown rain, it is understandable how *P. ramorum* could readily spread among oaks within a given location. It is harder to explain long-distance jumps between known sites with oak disease: What process vectored *P. ramorum* between oak trees in Cazadero and Boonville, Boonville and Brookings, Oregon, or sites on opposite sides of the Napa Valley? Aerial dispersal of spores in wind without rain can move spores up to a kilometer (Ristaino and Gumpertz 2000). However, only two of the 60 species of *Phytophthora* are known to have this kind of dispersal (Duniway 1983). None-the-less, given the range data on oaks, we are initiating wind tunnel studies to test for dispersal of *P. ramorum* sporangia by air without rain. In addition, anthropomorphic spread of infection cannot be ruled out. Ultimately, it also remains a primary research priority to investigate forested corridors between oak disease sites for the presence of infected foliar hosts serving as infection pathways.

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Sudden Oak Death: Disease Trends in Marin County Plots after One Year[1]

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Abstract

Sudden oak death has emerged as a major threat to the oak forests of California. In oaks and tanoak, this disease complex consists of a previously unreported fungus-like pathogen, *Phytophthora ramorum*, insects (bark and ambrosia beetles), and a secondary fungus, *Hypoxylon thouarsianum*. Species monitored in this study were coast live oak (*Quercus agrifolia*), California black oak (*Q. kelloggii*), and tanoak (*Lithocarpus densiflorus*). Disease progression plots were initiated in March 2000 to determine infection and mortality levels, symptomology, and changes in disease status. Plots were placed in two ecologically different sites in Marin County, China Camp State Park and a protected watershed of the Marin Municipal Water District (MMWD). Ten plots of 0.1 to 0.2 ha, selected to encompass the range of habitat types and species compositions found within these forests, were placed in each site. For all oaks and tanoaks, the following data were recorded quarterly for one year: diameter (dbh); presence/absence and abundance of seeps; presence/absence of *H. thouarsianum* fruiting bodies; presence/absence of bark and ambrosia beetles; and condition of the foliage. More than 750 oaks and tanoaks in these plots have been permanently tagged and geolocated using a global positioning system (GPS). Across China Camp State Park, independent and unbiased estimates of infection and mortality levels were acquired in summer 2001 using point-centered quarter sampling.

Apparent infection and mortality levels increased for the three species between March 2000 and March 2001. For coast live oak in China Camp, apparent infection levels increased from 35 percent in 2000 to 38 percent in 2001. In MMWD, these values were 16 percent in 2000 and 19 percent in 2001. Mortality of coast live oak rose from 8 to 15 percent in China Camp and 6 to 8 percent in MMWD during this period. California black oak in both sites exhibited apparent infection levels of 19 percent in 2000 and 27 percent in 2001. Apparent infection levels in tanoak rose from 40 to 55 percent in one year. Mortality also rose, from 12 to 15 percent. The point-centered quarter method yielded estimates of 30 percent for infection and 14 percent for mortality, for coast live oak. For California black oak, estimates were 21

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percent for infection and 16 percent for mortality. The role of bark and ambrosia beetles in this disease complex is unclear. Every symptomatic tree that died had been colonized by beetles in the plots prior to death. These insects have consistently been found in association with seeping areas on infected trees. Normally these bark and ambrosia beetles are associated with dying, dead, and broken trees. These interactions between an apparently novel pathogen, its host plants, and native insects represent new ecological associations, with unknown future consequences for these forests.

Introduction

A disease that appears to be caused primarily by a newly described pathogen, *Phytophthora ramorum* (Werres and others 2001), has infected many woody plant species in central and northern coastal California. This disease is referred to as sudden oak death syndrome, in reference to the rapid color change of foliage from green to brown over a period of weeks to months, in its final stages in oaks and tanoaks (Svihra 1999a). Prior to the isolation and description of this fungus-like pathogen as a species of *Phytophthora* (Garbelotto and others 2001), the causal agent of elevated tree mortality was unknown. This organism was subsequently shown to be the same species as a previously described pathogen infecting rhododendrons in Western European nurseries in the early 1990s (Werres and Marwitz 1997).

Tanoaks, *Lithocarpus densiflorus*, were first reported to be dying in California in 1995 (Svihra 1999b). Although a number of other species are now known to be hosts, the effects of the disease appear to be most severe for tanoaks and for several native oak species. *Phytophthora ramorum* is pathogenic on a number of species in the Fagaceae, including coast live oak, *Quercus agrifolia*, California black oak, *Q. kelloggii*, Shreve oak, *Q. parvula* var. *shrevei*, and tanoak. In addition, pinoak, *Q. palustrus*, and northern red oak, *Q. rubra*, are also susceptible in laboratory tests (Rizzo and others 2002). Native species in the families Ericaceae, Aceraceae, Hippocastanaceae, Rosaceae, Rhamnaceae, and Lauraceae have recently been shown to be hosts of the pathogen.

In California, the presence of the disease has been confirmed in forested areas from Big Sur, in Monterey County to southern Mendocino County, with major infestations in Marin, Sonoma, Monterey, and Santa Cruz Counties. An additional infestation in tanoak has been confirmed recently in Curry County, southwestern Oregon. The reasons for the apparently disjunct range of its geographic distribution are unknown.

When the field plots described in this report were established in March 2000, very little was known about the etiology of the disease in oaks and tanoaks. The most notable characteristics of sudden oak death syndrome were the apparently rapid death of large, mature trees, seeping (“bleeding”) of a dark, viscous exudate, typically on the lower trunk, and the association of large numbers of bark and ambrosia beetles (Coleoptera: Scolytidae) and fruiting bodies of *Hypoxylon thouarsianum* with the seeping areas of declining but still green trees.

These observations appeared to support a primary role for bark and ambrosia beetles (Svihra 1999c) and/or *H. thouarsianum* in tree death, in the absence of an identified pathogenic agent. There are two species of ambrosia beetles, *Monarthrum scutellare* and *M. dentiger*, that have been observed to tunnel into the sapwood of host trees. The western oak bark beetle, *Pseudopityophthorus pubipennis*, produces galleries in the phloem and outer bark of many oak species. These insects are opportunists, utilizing weakened, broken, and uprooted host trees (Furniss and Carolin 1977), and in natural forests, have only rarely been reported to attack living trees (Solomon 1995).

Speculations concerning anthropogenic causes, e.g., acid precipitation and air pollution, as well as climatic fluctuations associated with the El Niño and La Niña phenomena were also advanced. The absence of information on the basic etiology of sudden oak death syndrome motivated the research reported here. The goals of this study were to: 1) describe the symptoms and the order of their appearance, 2) determine a time course for symptoms of the disease and signs of associated organisms, 3) investigate the association of beetles and of *H. thouarsianum* in trees with bleeding cankers, 4) determine whether beetles were attacking apparently healthy trees, and 5) establish the time of first appearance of seeping cankers on symptom-free trees and the subsequent response of the trees.

Methods

Research plots to monitor symptom progression were established in March and April 2000 in two sites in Marin County; China Camp State Park (10 plots) near San Rafael and Marin Municipal Water District (10 plots), a protected watershed on the lower elevations of Mt. Tamalpais *(fig. 1)*. Both sites exhibit heavy levels of sudden oak death syndrome in some areas and light to no apparent infection in others. These two sites are approximately 12 km apart and differ somewhat in microclimate, elevation, and woody species composition. China Camp State Park (605 ha) is bordered by the city of San Rafael on the south and west and San Pablo Bay on the north and east. Study plots range from near sea level to slightly more than 200 m in elevation. The Marin Municipal Water District (MMWD) site is approximately 6 km from San Pablo Bay and 8 km from the Pacific Ocean. This site is bordered by Mt. Tamalpais State Park, Golden Gate National Recreation Area, and other forested land. Study plots were placed at elevations between 180 and 250 m. *Lithocarpus densiflorus* is present only in MMWD, although both *Q. agrifolia* and *Q. kelloggii* are found in both sites. Smaller numbers of two apparently resistant species, valley oak, *Q. lobata*, and blue oak, *Q. douglasii*, occur in China Camp State Park.

Symptom progression plots were not located at random, but were selected to encompass a range of habitat types, species compositions, and moisture regimes. Limiting consideration to the Fagaceae, the plots included coast live oak alone; coast live oak plus black oak; coast live oak, black oak, and valley oak; coast live oak, black oak, and tanoak; coast live oak and tanoak; and tanoak alone. Although these plots include a number of other woody species that have recently been shown to be either hosts for *P. ramorum* or to be susceptible to this pathogen in laboratory tests, the oaks and tanoak are the focus of this study.

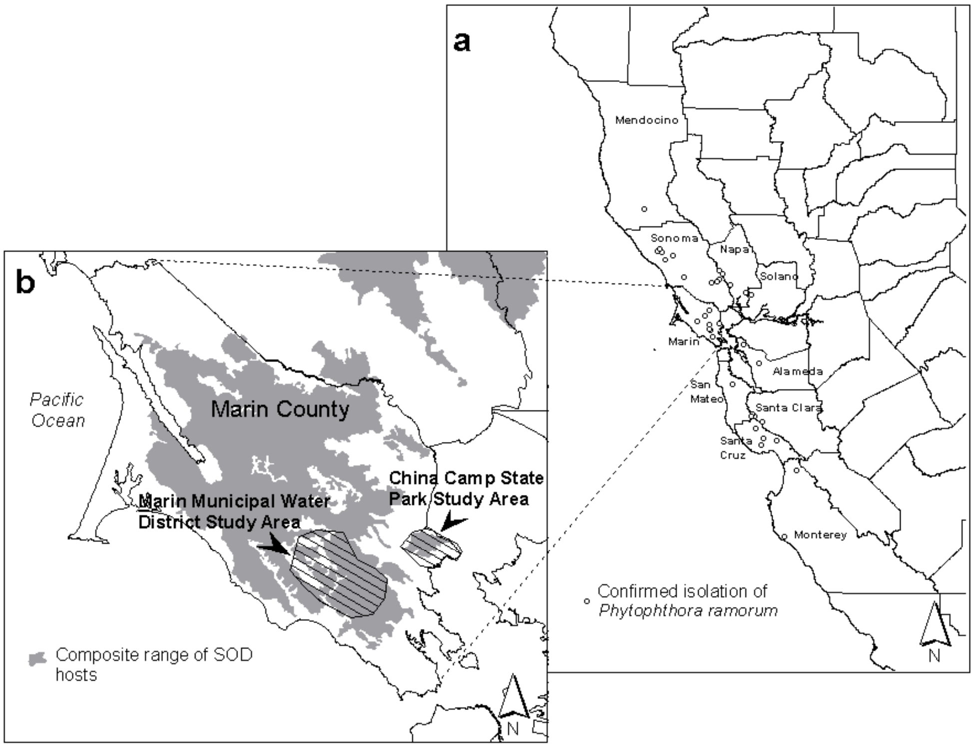

Figure 1—a) Distribution of confirmed cases of *P. ramorum* infection in coast live oak and tanoak in California, through August 2001. b) Locations of the permanent monitoring study sites in Marin County. Shaded areas indicate the composite range of hosts of *P. ramorum.*

In each of the 0.1 to 0.2 ha plots, the following variables were recorded for all oaks and tanoaks:

- Species
- Diameter at breast height (dbh)
- Presence/absence and abundance of seeps
- Presence/absence and abundance of fruiting bodies of *H. thouarsianum*
- Presence/absence, and age of bark and ambrosia beetle infestations
- Distribution of beetles in relation to seeping areas
- Condition of the foliage.

A tree was determined to be dead when its leaves had turned brown. Only trees that showed unambiguous evidence of bleeding cankers were counted in the assessment of mortality. *Phytophthora ramorum* has been repeatedly isolated from *Q. agrifolia*, *Q. kelloggii*, and *L. densiflorus* in the forests where these plots are located (see http://camfer.cnr.berkeley.edu/oaks). Individual trees in the plots were not tested for the presence of *P. ramorum*, but were instead characterized by the symptoms of sudden oak death described above (McPherson and others 2000). The only consistently reliable diagnostic methods presently available require that samples from an active canker be removed for culturing. Since cutting into trees is an invasive technique, trees in these plots were not sampled for the presence of *P. ramorum*. For the assessment of mortality at the initiation of the study in March 2000, trees were recorded as dead only if they showed unambiguous signs of the seeping associated with sudden oak death. Data from trees have been collected four times per year, since March 2000, giving five observation points by March 2001. A total of 760 oaks and tanoaks in these plots have been permanently tagged and geolocated using a global positioning system (GPS).

An independent assessment of infection and mortality levels for *Q. agrifolia* and *Q. kelloggii* was conducted in China Camp State Park in June to September 2001. The point-centered quarter plotless density estimation method (Cottam and Curtis 1956, Engeman and others 1994) was used to provide unbiased estimates of these variables using transect-based sampling across broad areas of this forest. The anchor point for each transect was located near the San Pablo Bay side of the park on a North-South axis, from which sampling points (nodes) were placed at 100 m intervals. The parallel transects were spaced approximately 500 m apart. A GPS reading was taken at the anchor point and at each node to allow for follow-up monitoring. The nearest *Q. agrifolia* or *Q. kelloggii* that fell within each 90^o quadrant (N, S, E, and W) around every node was permanently labeled and the same variables used for the permanent plots were recorded. The azimuth and distance from the node were recorded for use in GIS analysis. This provided a maximum of four host trees per sampling node. If a tree was more than 30 m from a node, that quadrant was considered empty.

Results

Trees exhibiting symptoms of sudden oak death, as well as recently killed trees, were widespread within the areas where the plots were located. Although the symptom progression plots were selected without regard for the presence of trees with symptoms, none was free of symptomatic trees. No trees recorded as having seeping cankers were observed to be free of this symptom on subsequent sampling dates, although seeps were difficult to detect during the dry months.

The percentage of symptomatic trees increased for all species monitored during the period of March 2000 to March 2001 *(table 1)*. For *Q. agrifolia* in China Camp State Park, the overall level of symptomatic trees was 35.4 percent in March 2000 and 38.6 percent in March 2001 *(table 1)*. Between-plot variation in the percentage of symptomatic coast live oaks ranged from 7 to 95 percent in 2000 and from 13 to 95 percent in 2001. In the MMWD plots, the overall percentage of symptomatic coast live oaks was 16.3 percent in 2000 and 18.9 percent in 2001. The between-plot range was 0 to 43 percent in 2000 and 0 to 48 percent in 2001.

Table 1—*Percentages of coast live oak, California black oak, and tanoak exhibiting the seeping symptom of sudden oak death syndrome in Marin Co. plots, March 2000 and March 2001.*

			Trees alive		**Trees alive and seeping**	
Site	Species	n	2000	2001	2000	2001
China camp	Coast Live Oak	293	92.5	86.7	35.4	38.6
MMWD	Coast Live Oak	214	94.4	91.6	16.3	18.9
MMWD	Tanoak	157	89.2	87.3	40.4	55.5
China Camp and MMWD (both sites)	California black oak	32	96.9	87.3	19.3	26.7
China Camp and MMWD (both sites)	Coast Live Oak	507	93.3	88.8	27.3	30.0

Every *Q. agrifolia* that died between March 2000 and March 2001 had symptoms of sudden oak death syndrome. The overall mortality for *Q. agrifolia* in China Camp State Park rose from 7.5 percent (22 trees) in 2000 to 14.7 percent (43 trees) in 2001 *(table 2)*. Variation in mortality by plot was 0 to 14.3 percent in 2000 and 0 to 28.6 percent in 2001. In MMWD, overall mortality of *Q. agrifolia* was 5.6 percent (12) in 2000 and 8.4 percent (18) in 2001. Mortality varied among plots from 0 to 23 percent in 2000 and from 0 to 35.9 percent in 2001. For the China Camp State Park plots, 7.8 percent (21) of the trees that were alive in March 2000 were dead by March 2001. In MMWD, 3 percent (6) of *Q. agrifolia* died after one year. For *Q. agrifolia* summed across both sites, 5.7 percent (27) of the trees died during this period.

Table 2—*Mortality of coast live oak, California black oak, and tanoak in Marin Co. plots, March 2000 and March 2001. Only trees with seeping cankers were included in these figures.*

Species	**Site**	**Dead trees pct**	
		2000	2001
Coast live oak	China Camp	7.5	14.7
	MMWD	5.6	8.4
Tanoak	MMWD	12.1	14.6
California black oak	China Camp plus MMWD	3.1	6.3
Coast live oak	China Camp plus MMWD	6.9	12.0

The percentage of symptomatic *L. densiflorus* trees in MMWD increased from 40.4 percent in 2000 to 55.5 percent in 2001. Every tree recorded as dead in March 2000 exhibited the seeping symptom. The percentage of symptomatic trees among plots varied from 20 percent to 63.6 percent in 2000 and from 23.3 percent to 77.8 percent in 2001. Mortality among *L. densiflorus* rose from 12.1 percent (19) in 2000 to 14.6 percent (23) in 2001. The variation in mortality among plots was 0 to 23 percent in 2000 and 0 to 25.6 percent in 2001. Between March 2000 and March 2001, 2.5 percent (4) of the *L. densiflorus* in the plots died.

Quercus kelloggii, although not uncommon in both study sites, is under-represented in the plots (32 out of 760 trees). For this reason, data from both sites were pooled. The percentage of symptomatic trees rose from 19.3 percent in 2000 to 26.7 percent in 2001. One tree died during the year, doubling the mortality level to 6 percent. The relative scarcity of this species in the plots precludes meaningful site-level discussion.

The abundance of symptomatic *Q. agrifolia* in China Camp State Park varied through the monitoring year *(fig. 2)*. The decline in the total number of asymptomatic trees reflects the increasing number of symptomatic trees that died, plus those newly identified as seeping. For *Q. agrifolia* in MMWD *(fig. 3)*, the trend is similar. When symptomatic and dead *L. densiflorus* are compared, the numbers of dead trees increased slightly, while the numbers of symptomatic trees increased more dramatically *(fig. 4)*.

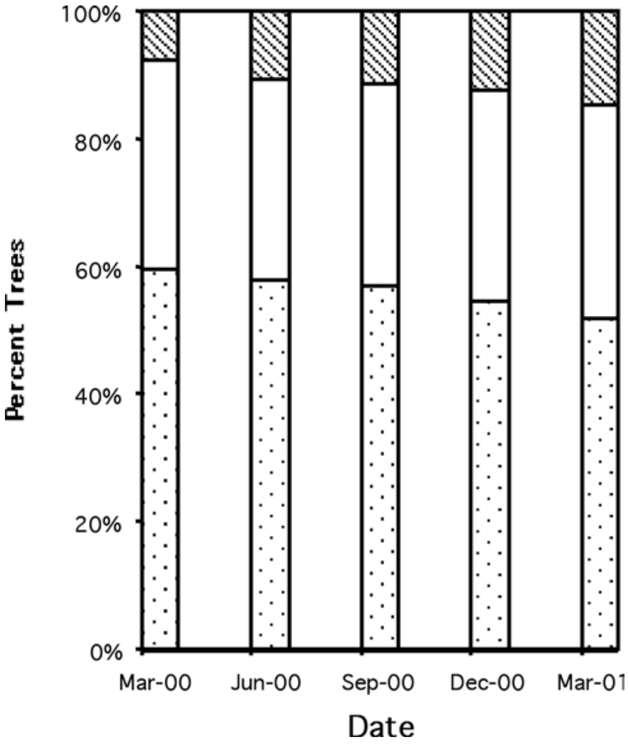

Figure 2—Percentages of coast live oaks in China Camp State Park study plots that are asymptomatic (stippled bars), have seeping cankers (clear), and are dead (cross hatched) at five sampling dates.

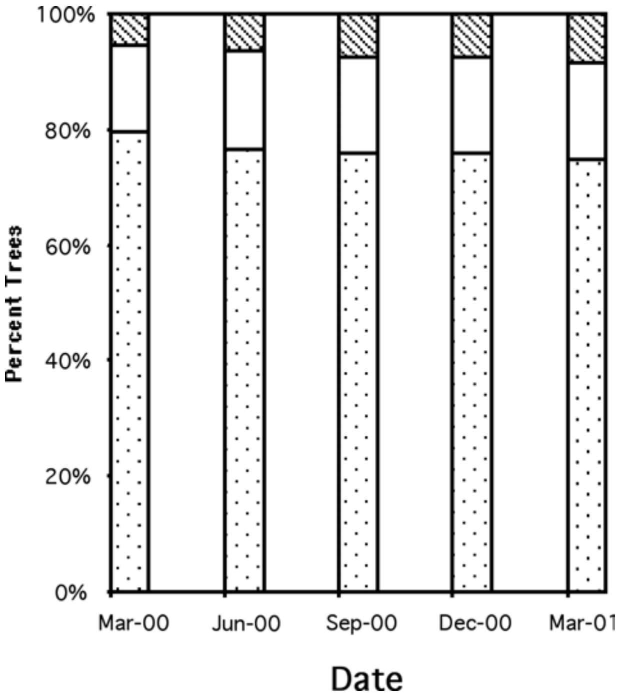

Figure 3—Percentages of coast live oaks in Marin Municipal Water District study plots that are asymptomatic (stippled bars), have seeping cankers (clear), and are dead (cross hatched) at five sampling dates.

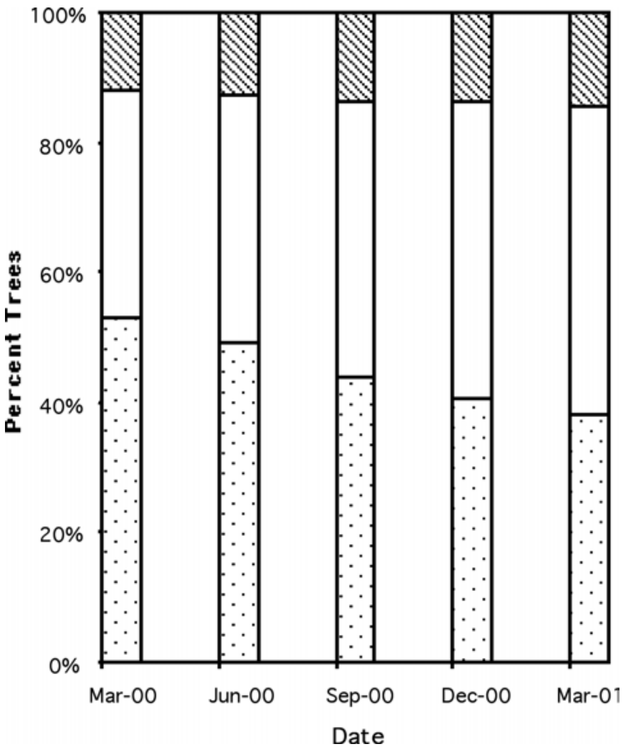

Figure 4—Percentages of tanoaks in Marin Municipal Water District study plots that are asymptomatic (stippled bars), have seeping cankers (clear), and are dead (cross hatched) at five sampling dates.

The association of bark and ambrosia beetles with symptomatic trees appears to be more consistent in *Q. agrifolia* than in L. *densiflorus*. For *Q. agrifolia* in China Camp State Park, the percentage of seeping trees that had been colonized by bark beetles alone was 19.8 percent (19) in March 2000 and 11.2 percent (11) in March 2001 *(table 3)*. Among the symptomatic *Q. agrifolia*, those that exhibited both beetles and fruiting bodies of *H. thouarsianum* constituted 26.0 percent (25) in 2000 and 47.9 percent (47) in 2001. All 21 *Q. agrifolia* in China Camp State Park plots that died between March 2000 and March 2001 had been colonized by bark beetles while the foliage was green and apparently functional.

Table 3—*The co-occurrence of bark beetles and* H. thouarsianum *with seeping trees, March 2000 and March 2001. Numbers in boldface denote the presence of bark and ambrosia beetles in seeping trees. Where percentages are reported in the text, these are in reference to the total number of seeping trees.*

Signs and symptoms associated with sudden oak death syndrome	**Coast live oak, China Camp**		**Coast live oak, MMWD**		**Tanoak, MMWD**	
Year	2000	2001	2000	2001	2000	2001
Number of living trees	271	254	202	196	140	137
Number of Seeping Trees	96	98	33	37	56	76
Seeping only	46	40	18	24	49	62
Beetles only	0	1	1	0	1	0
Hypoxylon *only*	5	3	1	0	0	0
Seeping + Beetles	**19**	**11**	**10**	**2**	**5**	**7**
Seeping + *Hypoxylon*	6	1	1	1	1	0
Beetles + *Hypoxylon*	1	0	0	0	0	0
Seeping + Beetles + *Hypoxylon*	**25**	**47**	**4**	**10**	**1**	**6**

In MMWD, the percentage of seeping *Q. agrifolia* that had been colonized by bark beetles but which did not exhibit signs of *H. thouarsianum* was 30.3 percent (10) in March 2000 and 5.4 percent (2) in March 2001. The fraction of seeping trees that exhibited both beetles and fruiting bodies of *H. thouarsianum* constituted 10.8 percent (4) in 2000 and 27.0 percent (10) in 2001. All six symptomatic *Q. agrifolia* that died during this period were colonized by bark beetles prior to dying. These data show that bark beetles and *H. thouarsianum* fruiting bodies are rare on living trees in the absence of the seeping cankers characteristic of *P. ramorum*. For all *Q. agrifolia* monitored (both sites), one tree was found colonized by beetles in the absence of the seeping symptom in March 2000 and in March 2001 *(table 3)*. The reproductive structures of *H. thouarsianum* are commonly seen on dead stems and branches on living oaks, fallen logs, and standing dead oaks. However, in the absence of bleeding cankers, the number of living *Q. agrifolia* in all the plots exhibiting these fruiting bodies was six in March 2000 and three in March 2001. These trees were characterized by generally poor appearance and the fruiting bodies of other fungi were often present.

The association of seeping *L. densiflorus* with bark beetles was weaker than for *Q. agrifolia*. In March 2000, 10.2 percent (5) and in March 2001, 11.3 percent (7) of seeping trees in the plots had been colonized by these insects *(table 3)*. The percentage of seeping *L. densiflorus* with the combination of beetles and *H.*

thouarsianum fruiting bodies was 2.0 percent (1) in 2000 and 9.7 percent (6) in 2001. One *L. densiflorus* was identified with beetles in the absence of the seeping symptom.

The point-centered quarter analysis for the forest in China Camp State Park provided estimates for both alive symptomatic (30 percent) and dead (14 percent) *Q. agrifolia* (n=174) in August 2001 that are broadly consistent with those derived from the symptom progression plots, 38 percent and 13 percent, respectively, in March 2001. For *Q. kelloggii* (n=45), the point-centered quarter estimates for symptomatic (21 percent) and dead (16 percent) trees appear similar to the plot-based results of 27 percent and 6 percent, respectively.

Discussion

Sudden oak death is not as sudden as implied by both the name and general impressions. Once seeping cankers develop, trees may live for two years or more, although they may also die sooner than this. Observations are yet insufficient to fully address this issue. Trees may survive for several years or more once seeping cankers appear, but whether they can recover from an infection is unknown. There is a general sequence of the appearance of symptoms and associated organisms. For *Q. agrifolia* and *Q. kelloggii*, bleeding cankers precede foliage symptoms and the appearance of *H. thouarsianum* and bark beetles (McPherson and others 2000). Bark and ambrosia beetle colonization clearly follows the appearance of bleeding cankers. The longer a tree has seeping cankers, the greater is the likelihood of colonization by beetles. *Hypoxylon thouarsianum* is apparently present as an endophyte in a majority of *Q. agrifolia* surveyed in northern California (Chapela, personal communication). As the production of fruiting bodies is associated with drying out of wood infected by this fungus, their presence on a tree with green foliage indicates that its health has been impaired. For *L. densiflorus*, the initial symptom is often flagging of branch tips and scattered leaf death, which is then followed by a sequence of symptoms similar to those of *Q. agrifolia* (McPherson and others 2000). Because our estimates for numbers of symptomatic *L. densiflorus* are based on the presence of seeping cankers, this probably underestimates the true level of symptomatic trees. Changes in the foliage of the deciduous *Q. kelloggii* are less reliable indicators of sudden oak death syndrome, but the other symptoms also follow the pattern observed for *Q. agrifolia*.

The emergence of new diseases, or of newly recognized diseases, appears to be a feature of the modern global economy. Once a pathogenic agent becomes established in populations of susceptible host plants that lack evolved resistance, the effects can be catastrophic. Examples of introduced diseases in North American forests include chestnut blight, Dutch elm disease, white pine blister rust, beech bark disease, and pitch canker, to name the most obvious. The symptom progression plots described here were not started prior to the introduction of *P. ramorum* and development of sudden oak death. The mix of low to high infection levels they represent can illustrate different stages in the development of the epidemic. The increasing numbers of both symptomatic (seeping) and dead trees in these plots, even in forests where trees were observed dying more than five years ago, indicates that trees are still being infected. It is also possible that trees inoculated prior to the establishment of these plots developed cankers much later. Information on baseline, pre-epidemic mortality levels in these forests is lacking, and as a result, the true effects of this epidemic may be difficult to quantify. However, monitoring forest stands at different stages in the course of this disease provides an opportunity to understand forest dynamics under the influence of this apparently novel pathogen.

Bark and ambrosia beetles are found in association with *Q. agrifolia*, *Q. kelloggii*, and *L. densiflorus* trees that have symptoms of sudden oak death. This association with only the seeping areas on trees that have asymptomatic foliage suggests a new relationship between these insects and their living host trees, mediated by a novel pathogen. Their normal substrate is recently killed trees, fallen or standing, or individual dead branches on living trees. These insects have not been previously reported to colonize the main stem of trees with apparently healthy, green foliage. Both species of ambrosia beetles are reported to be rare (Chamberlain 1960), yet large increases in their populations have occurred where the epidemic is present (Svihra 1999c). The scarcity of these organisms on *Q. agrifolia* trees that do not show symptoms of sudden oak death is in contrast to their abundance on infected trees *(table 3)*. The ability of these beetle species to infest and kill disease-weakened trees when present in large numbers is unknown. However, in the case of other scolytids, large populations produced during epidemics enable the beetles to overcome tree defenses and infest apparently healthy trees (Wood 1982). It is well documented that bark beetles more readily kill trees infected with root pathogens than uninfected trees (Goheen and Hansen 1993). Our preliminary data show that during the one year of monitoring *Q. agrifolia* trees, 1) bark and ambrosia beetles were scarce in the absence of sudden oak death syndrome, as detected by the presence of seeping cankers, 2) the trees that became colonized by these beetles during the year of monitoring also exhibited seeping as the initial symptom of sudden oak death syndrome, and 3) all trees with sudden oak death syndrome that died were previously colonized by these beetles and also had fruiting bodies of *H. thouarsianum* on the main stem. Despite concerted efforts to find bark beetles in trees that lacked symptoms of sudden oak death syndrome, this remained a rare event.

Observations in MMWD plots indicate that the abundance of bark and ambrosia beetles on infected trees varied considerably among sites. This variation may be due to local population size and site factors such as local tree species composition. It is also likely that the variation in bark beetle population levels at different sampling times reflects seasonal variation in temperature and rainfall.

Data collected from the symptom progression plots will be coupled with multispectral reflectance data collected from remote imaging (Kelly and McPherson 2001). The goal is to correlate tree health status characterized by symptoms obtained from ground observations, such as seeping and beetles, with the remote imagery. Research continues to explore the possibility of detecting trees with sudden oak death syndrome prior to the appearance of visible foliage symptoms.

Conclusions

In forested areas where sudden oak death syndrome and the *P. ramorum* pathogen have been established for several or more years, we have identified a number of trees that were symptom-free at the beginning of the study and subsequently developed the initial seeping symptoms. The fact that these apparently healthy trees developed symptoms recently argues for caution in ascribing the presence of symptom-free trees in such stands to disease resistance.

Although the role of bark and ambrosia beetles in tree death is unclear, several lines of evidence suggest that these insects may hasten this process. The percentage of *Q. agrifolia* trees with symptoms of sudden oak death that were colonized by these beetles, singly or in combination with *H. thouarsianum*, while maintaining green foliage, varied from 42.4 percent to 59.2 percent in 2000 and 2001. This is in contrast to the scarcity of these beetles in non-symptomatic trees. Every *Q. agrifolia* that died with symptoms of sudden oak death syndrome had been colonized by beetles prior to dying. Since bark beetles are associated with the decline and death of numerous tree species following infection by pathogenic fungi, this association is consistent with other tree-pathogen interactions (Goheen and Hansen 1993).

The analysis of these plots confirms the impression that the distribution of this disease complex is patchy. This pattern may be a consequence of the relatively early stage of the epidemic in forests of coastal California. It is also possible that the presence of other host species influences the level of infection occurring in oaks and tanoak.

The symptomology in *Q. kelloggii* appears to be similar to that in *Q. agrifolia*,[6] although the results presented here are not sufficient to document this. *Lithocarpus densiflorus* populations appear to be more susceptible to *P. ramorum* than the oak species studied. This conclusion is suggested by the higher level of infection found in these plots and by the high levels of sudden oak death symptoms observed in sapling *L. densiflorus* (McPherson, personal observation). On the other hand, the oak species are relatively scarce in the understory, and thus under-represented in the symptom progression plots.

These study plots were initiated when the known geographic range of the epidemic included Big Sur to the south and Sonoma County to the north. This distribution indicates that the pathogen had already been established for some unknown period of years. Thus, one year of data is insufficient for any trends to be detected. Yearly climatic variation may alter such variables as the mean response of trees to *P. ramorum*, beetle population size and species composition, and the transmission of disease propagules. Based on current apparent infection levels and observed mortality levels, significant mortality is likely for years to come, even in areas where the disease appears to have been established for five or more years.

The plots described here will be monitored quarterly for the next several years. These plots will also be used for additional ecological assessments of long-term vegetation changes that are likely to follow this epidemic. As eastern North American oak species appear to be highly susceptible to this pathogen, the response of the California forests may be predictive of forests in other regions if the pathogen becomes established elsewhere.

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Phytophthora ramorum and Sudden Oak Death in California: III. Preliminary Studies in Pathogen Genetics[1]

Matteo Garbelotto,[2] David M. Rizzo,[3] Katie Hayden,[2] Monica Meija-Chang,[2] Jennifer M. Davidson,[3] and Steven Tjosvold[4]

Abstract

Sudden oak death (SOD) has been shown to be caused by a new species of *Phytophthora*, *P. ramorum*. A basic understanding of the genetics of *P. ramorum* is critical to any management strategy. We have initiated a number of studies to examine species concepts, population biology and mating behavior of the pathogen. Based on a number of morphological features (e.g., a combination of deciduous sporangia and chlamydospores), the *P. ramorum* does not match any of the currently described species of *Phytophthora*. Sequences of the internal transcribed spacer (ITS) of nuclear ribosomal DNA were identical for isolates from *Lithocarpus densiflorus*, *Quercus* spp., *Rhododendron* sp., *Vaccinium ovatum*, *Umbellularia californica*, and *Aesculus californica*. The sequences were also identical to a recently described species from Europe, *P. ramorum*. Based on ITS sequences, the closest species to *P. ramorum* is *P. lateralis*; ITS sequences between the two species differ by 12 nucleotides. We are now examining the population structure of *P. ramorum* using amplified fragment length polymorphisms (AFLPs) to determine variability within pathogen populations. This information will provide insights into whether *P. ramorum* is an exotic pathogen and whether sexual recombination is taking place in California populations. Finally, the use of genetic data allows for the development of species specific diagnostic probes. PCR primers based on the ITS region have been used to facilitate the rapid identification of the pathogen from plant tissue.

Introduction

The pathogen responsible for lethal stem cankers leading to the extensive dieback of California black oak (*Quercus kelloggii*), California coast live oak (*Q. agrifolia*), Shreve's oak (*Q. parvula var. shrevei*) and Tanoak (*Lithocarpus densiflora*) is easily identifiable as a species within the genus *Phytophthora* (Garbelotto and others 2000, Rizzo and others 2002a). A pathogen with similar morphology has also been shown to be responsible for extensive foliar blight and necrosis, often leading to twig and branch die-back, in several plant species including

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California bay laurel (*Umbellularia californica*), madrone (*Arbutus menziesii*), and *Rhododendron spp*. (Rizzo and others 2002b).

While the presence and morphology of sporangia (specialized reproductive structures containing motile zoospores) and chlamydospores (rounded, thick-walled resting propagules) provide sufficient information for the taxonomic placement of the pathogen within the genus *Phytophthora*, there is no obvious match with any other of the sixty known species belonging to this genus. The presence of sympodial semipapillate and caducous sporangia combined with the formation of terminal and intercalary chlamydospores is unreported within the genus (Garbelotto and others 2000, Rizzo and others 2002a). Only recently, similar traits have been described for a new *Phytophthora* species, *P. ramorum*, isolated from ornamental rhododendron plants in Germany and the Netherlands (Werres and others 2001).

While morphological descriptions can be diagnostic for many *Phytophthora* species, they are often equivocal. The problem is compounded by the variability in spore and propagule production as well as in somatic growth often observed among isolates within a species. This variability has been shown to be linked to intraspecific genetic variability, to different life histories (e.g., climate and hosts in which they have lived), and to growth medium and temperature conditions (Erwin and Ribeiro 1996, Brasier and others 2000).

In this paper, we describe: a) how species determination of the new SOD pathogen and its evolutionary placement within the genus *Phytophthora* was obtained through DNA-based phylogenetic analysis; b) how extremely species-specific DNA sequence data was used to design molecular probes that were then used with the aid of the polymerase chain reaction (PCR) to study the presence and distribution of the pathogen in the environment (e.g. plant hosts, soil, water); and finally, c) how multilocus genetic data is being generated using a technique called amplified fragment length polymorphisms (AFLP) (Vos and others 1995) to determine the genetic variability and the population structure of the pathogen. Based on an overall analysis of the above preliminary data, we suggest reasonably supported hypotheses regarding the biology of this pathogen.

Materials and Methods

Isolate Selection and Growth Conditions

Phytophthora ramorum isolates were chosen to represent a broad variety of both geographic locations and hosts. A few areas were selected to be sampled more intensively. *Phytophthora* isolates were kept on potato dextrose agar or 5 percent V8 agar media at 22° C. For DNA extractions, isolates were grown in 100 mL of potato dextrose broth or V8 broth (Erwin and Ribeiro 1996) in Erlenmeyer flasks. Flasks were kept on a shaker at 22° C for approximately 21 days. The material was harvested by vacuum-aided filtration on filter paper. Hyphal material was then frozen and lyophilized overnight.

DNA Extractions

DNA extractions were performed using the protocol described by Garbelotto and others (1998) amended in the following way. Instead of performing an ethanol precipitation of nucleic acids, the Gene Clean II kit (Bio101, Carlstad, CA)[2] was employed, according to the manufacturer's directions. In each extraction, 10 uL of glassmilk were employed. DNA was finally resuspended in 35 uL of PCR water (Garbelotto and others 1993).

PCR Reactions, Sequencing, and AFLPs

The internal transcribed region (ITS) of the nuclear ribosomal operon was amplified in 50 uL volume reactions by 35 cycles of polymerase chain reaction (PCR) using primers ITS1 and ITS4 (White and others 1990) as described elsewhere (Garbelotto and others 1996). Four uL of each PCR product were loaded on a 1.5 percent agarose gel and electrophoresed for 1h and 30m at 4V/cm. Gels were stained with a 15 m Ethidium bromide wash followed by a 10 min rinse with water. Visualization of the gels was obtained with a digital camera and the software Kodak II. Positive amplifications were cleaned of all PCR reagents by using Qia-quick purification kit (Qiagen, Valencia, CA) and the pure DNA was sequenced with an automated ABI sequencer. Both DNA strands were sequenced for each isolate. Quality of each sequence was assessed by visual inspection of sequence chromatograms and congruity of sense and anti-sense DNA strands. Chromatograms were also inspected for the presence of double peaks, a feature that may indicate the presence of heterozygous ITS sequences. ITS heterozygosity is expected in first generation hybrids between two species characterized by divergent ITS sequences.

AFLPs were performed as recommended by the manufacturer of the AFLP microorganism kit (Invitrogen, Grand Island, NY). Visualization of AFLPs was obtained by polyacrylamide electrophoresis in an automated ABI 371 sequencer machine (Applied Biosystems, Foster City, CA). In each lane, both the molecular standard GeneScan (TM)-500 ROX(TM) Molecular Standard, and the final AFLP amplification product from each selected isolate. The final AFLP product was obtained using various primer combinations. The date here presented was obtained by using the primers EcoRI+GTA labeled with FAM and unlabeled MseI+A primer. Loading of the molecular standard and of the final product in the same lane allows for an unequivocal sizing of each AFLP fragment.

Sequence Alignment, Phylogenetic, and AFLP Analyses

Sequence alignments inclusive of the ITS1, ITS2 and 5.8S regions were obtained automatically with the program Sequencher and then manually corrected. The overall alignment deposited in GenBank by Cooke and others (2000) was used for phylogenetic placement of the new *Phytophthora* species. Phylogenetic analyses were performed using both the heuristic and the distance option in Phylogenetic Analysis Using Parsimony (PAUP) (Swofford 2000). Default settings were used for the heuristic search and the Neighbor Joining (NJ) algorithm was used for the distance search. Both methods yielded similar results and only the phylogenetic tree obtained by the heuristic search is here displayed and discussed *(fig. 1)*.

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[2] Mention of trade names or products is for information only and does not imply endorsement by the U.S. Department of Agriculture.

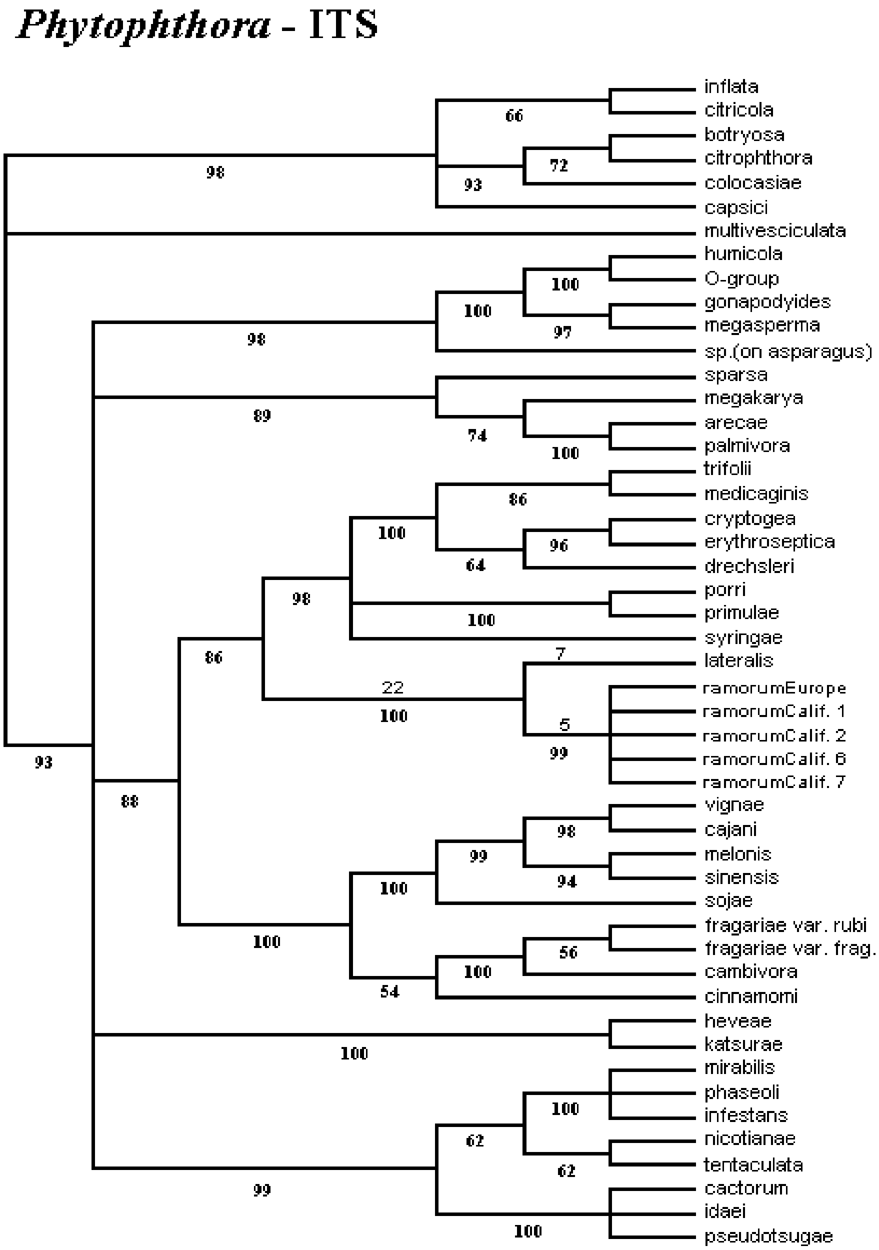

Figure 1—Cladogram showing phylogenetic positioning of the new *Phytophthora* species. The tree was obtained by parsimony analysis using the heuristic search option on PAUP (random addition sequence), and is one of 12 most parsimonious trees. Gaps were treated as missing, 860 characters were employed in the analysis. Tree parameters are as follows: consistency index=0.570, rescaled consistency index=0.834, homoplasy index=0.430, tree length=960. Boostrap values, shown in bold under branches, were obtained by 1000 replicates of the "fast" stepwise addition method. Branch lengths of terminal taxa are not shown, but there were no differences between *P. ramorum* and isolates from California.

AFLP bands were scored as present (1) or absent (0) for each isolate. The resulting binary matrix was transformed into a distance matrix using the Jaccard's coefficient of similarity. This transformation is necessary to reduce the error caused by the dominant nature of the AFLP markers as described in Garbelotto and others (1998). The resulting similarity matrix was then translated into a distance cladogram by using the neighbor-joining algorithm in PAUP. The tree was rooted by using the AFLP profile from an isolate of *Phytophthora lateralis*, the only close relative to the new species (see results below).

PCR Primer Design, Optimization of PCR Conditions, and Environmental Sampling

The alignments employed in the phylogenetic analyses were used to identify regions of sequence divergence (e.g., presence/absence of indels and base substitutions) between *Phytophthora ramorum* and all other *Phytophthora* species for which ITS sequences were available. Using the web-based Primer3 application (http://www.genome.wi.mit.edu/genome_software/other/Primer3.html) four specific PCR primers were designed. The first set of primers (Phyto1 and Phyto4) was designed to amplify a 687 BP fragment of the ribosomal operon of the new *Phytophthora* species. This fragment includes portions of the ITS1 and ITS2 and the entire 5.8S region. The second set of primers (Phyto2 and Phyto3) were designed to amplify a 291 BP portion of the ITS2 region, fully nested within the Phyto1-Phyto4 amplicon.

$MgCl_2$ concentration and annealing temperature were optimized through sequential amplification of identical or comparable DNA extracts. Both the specificity and the sensitivity of the approach needed to be maximized. Cross reactivity with other *Phytophthora* species was checked by amplification of pure DNA extracts from the following species; *P. citricola, P. cinnamomi, P. cryptogea, P. cambivora, P. drechsleri, P. infestans, P. "ilicis*-like,*" P. pseudotsugae, P. megasperma, P. cactorum, P. capsici, P. megasperma f. sp. glycinea, P. bohmeriae, P. parasitica, P. erythroseptica, P. nicotianae,* and *P. lateralis.*

To maximize sensitivity, a nested PCR approach was devised. After 35 cycles of PCR using primers Phyto1 and Phyto4, the PCR product was diluted a hundred fold and used as a template for 35 cycles of nested PCR with primers Phyto2 and Phyto3. Agarose electrophoresis and Ethidium bromide staining were used as described above to visualize intermediate and final products.

Environmental sampling was conducted by extracting DNA as described above from symptomatic (e.g. cankered or necrotic) plant material. Leaves, wood, oozing sap from cankers, and bark of several plant species were tested. Water samples were processed by collecting 50 ml of water from either streams or rainwater, centrifuging them at 3,000 rpm for 15 min, and by collecting 1 ml from the bottom of the tube with a micropipette. The collected liquid was then placed in an Eppendorf tube and centrifuged for 3 min at 15,000 rpm. Approximately 200 uL were collected with a micropipette from the bottom of the tube and transferred to a new tube. DNA extractions were performed as described above. Soil was soaked in water overnight. The wash water was collected in 50 ml tubes and treated as described above. Live isolations on PARP medium were often performed from the same substrate to compare the sensitivity of the two methods.

Results and Discussion

Phylogenetic Analysis

All 12 sequenced isolates of *Phytophthora ramorum* from 6 host species (California coast live oak, tanoak, rhododendron, huckleberry, bay laurel and buckeye) and 3 California counties (Marin, Napa, Sonoma) had identical ITS sequences *(fig. 1)*. The ITS sequence of the California isolates was also a perfect match with the sequence of European *Phytophthora ramorum* isolates obtained from foliar blotches and branch and twig cankers on *Rhododendron* spp. This phylogenetic placement is therefore in agreement with our preliminary observations, which indicated a striking morphological similarity between isolates from the two continents.

While identical ITS sequences are suggestive of conspecificity between the European and American populations, it should be noted that evolution in the ITS region is highly variable and taxon-dependent. There are cases in which different species have identical ITS (O'Donnell, personal communication), and cases in which populations of the same species from different regions of the world have different ITS sequences (Garbelotto, personal observation).

The only close relative *(fig. 1)* of *P. ramorum* is *P. lateralis*, an aggressive pathogen of *Chamaecyparis lawsoniana* (Port-Orford cedar) thought to have been introduced in the American Pacific Northwest in the early 1900s (Hansen and others 2000). While *P. ramorum* and *P. lateralis* share similar climatic preferences (they both seem to thrive in cooler temperatures), and some morphological features, there are three striking differences: 1) *P. lateralis* is mostly found in the roots and root collar of infected trees, while *P. ramorum* appears not to infect trees below the soil line. 2*) P. ramorum* appears to have a significant aerial phase as suggested by infections on leaves and by cankers found up to 20 m from the ground. This appears as a consequence of the caducous sporangia of *P. ramorum*. Only rarely are the sporangia of *P. lateralis* caducous. 3) *P. lateralis* is only found on two tree species (Port Orford cedar and occasionally Pacific Yew), while *P. ramorum* is found on at least 14 species representing 8 plant families.

AFLP Analysis

The primer combination produced 112 polymorphic fragments. Fragments that were ambiguous or parsimony uninformative (e.g., one fragment present in one or two individuals and absent in all others) were excluded from the analysis. A total of 63 characters were thus employed. The sample size is currently too small to make definitive conclusions based on these preliminary data. The presence of several polymorphic alleles suggests that *P. ramorum* is not a clonal species. Nonetheless, most of the variability in our data was represented by the European isolates, while little genetic variation was detected in the California population. The reduced genetic variability is in agreement with the hypothesis of an introduced microorganism.

Using *P. lateralis* as the outgroup *(fig. 2)*, it appears that European and California *P. ramorum* isolates are representatives of two different populations. This is supported by a 100 bootstrap value of the branch separating isolates from the two continents. The topology of the NJ tree could be explained in at least three ways: 1) the two populations are genetically isolated, but belong to the same species; 2) the two populations represent two species recently evolved from a common ancestor, and

3) the sampled individuals are representatives of the same population, but the oversampling of a single genotype, due to its successful spread throughout California, results in an apparent separation of the two populations. This final hypothesis would require the presence of individuals that may have been moved from one continent to the other. One *P. ramorum* isolate from Marin County (Pr-3) was strongly associated with the European isolates. Further studies need to verify whether such an isolate may represent a potential link between continents.

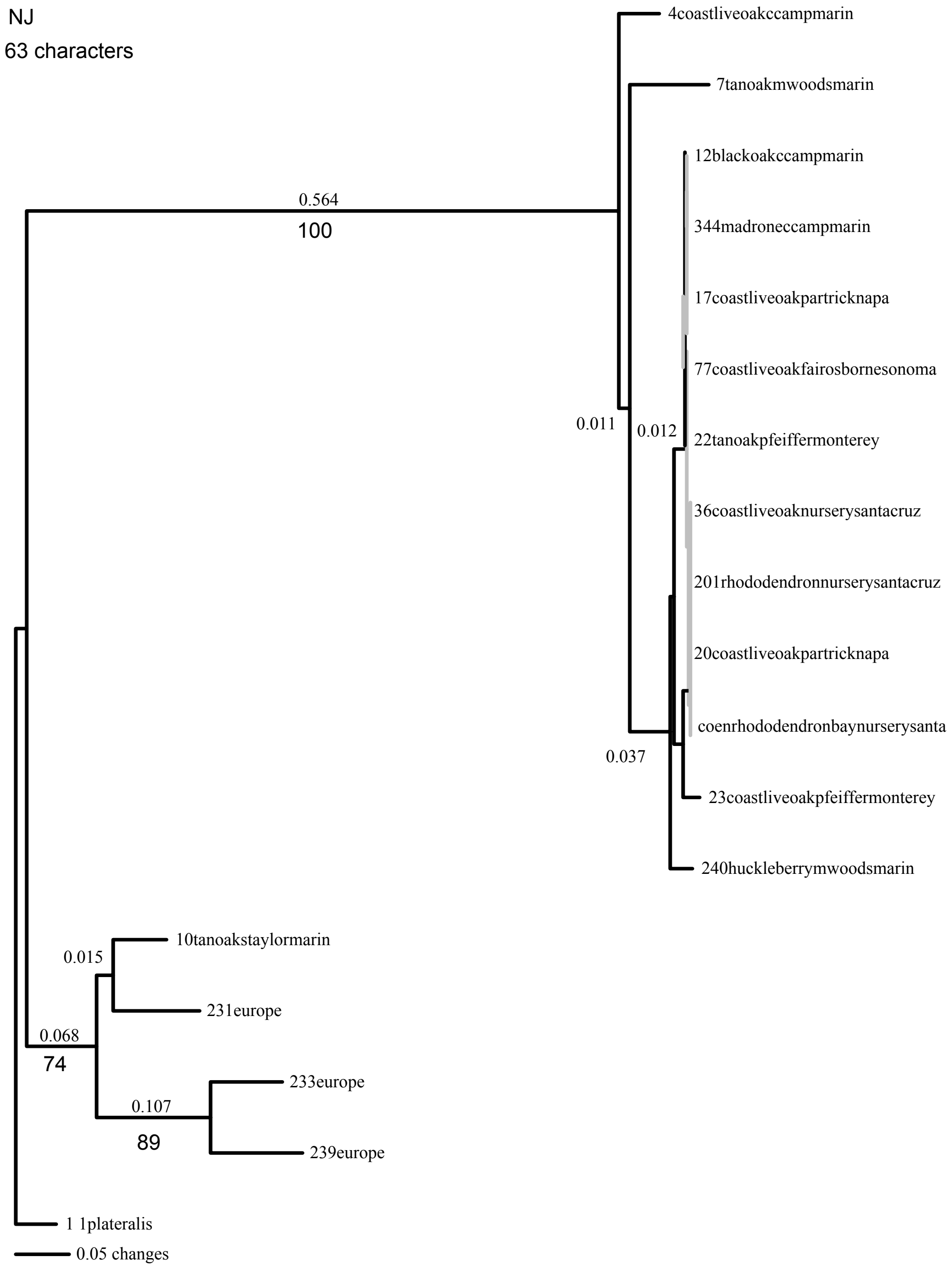

Figure 2—Neighbor Joining (NJ) phylogram obtained by analysis of the AFLP data. NJ distances greater than 0.01 are shown above branches. Bootstrap support values obtained by 1,000 replicates are shown under branches, when larger than 50.

There was no significant structuring of the California population based on host or location. This is in agreement with the hypothesis that *P. ramorum* was introduced recently on the West Coast of the U.S.A, and has had no time to diversify yet. Lack of structuring in our data could also be explained if *P. ramorum* were strictly clonal, The presence of some polymorphisms seems to suggest though that *P. ramorum* is not strictly clonal. One possible scenario explaining our data is that of multiple introductions (hence the lack of pure clonality) followed by the successful spread of only one or two individuals. It is interesting to observe that most of the variability in California is found in Marin County, the area where the disease was first reported.

More primer combinations and larger sample size are necessary to draw final conclusion on the genetic relatedness of European and California *P. ramorum* populations as well on the genetic structure of populations within California. Molecular analysis will also need to be supported by pathogenicity and mating tests.

These preliminary data though strongly suggest that in epidemiological terms, *P. ramorum* moves from one host to the other. The NJ tree, in fact, shows no clear separation between isolates on oaks and on non-oaks. On the contrary, isolates from all species are intermingled. Sporangia and chlamydospores of *P. ramorum* have been commonly found on bay leaves, but they are yet to be found on infected oak trees. For this reason, we suggest that infestation of a site may start with infection of the foliar hosts. This infection may lead to a build-up of the inoculum in the area and to successive infection of oaks. If this hypothesis were correct, most infected oaks would not be in pure oak stands, but in stands where foliar hosts such as bay or madrone are present. Our preliminary observations seem to corroborate such hypothesis.

Both tanoak stems and leaves appear to be infected by the pathogen. We believe the presence of both types of available infection sites, combined with a high genetic susceptibility are two of the key factors that may explain the high impact of *P. ramorum* on tanoak (Garbelotto and others 2000, Rizzo and others 2002a).

DNA-based Diagnostics

Our specific primers were extremely successful in identifying the pathogen, even when it was not detected by culturing. Hosts such as bay, madrone, buckeye, and the susceptibility of tanoak leaves were actually discovered thanks to positive PCR-based diagnosis (Rizzo and others 2002b). The nested technique greatly enhanced the sensitivity of our assays. For instance on a total of 89 leaf samples of unknown status 18 positive samples were added by the nested PCR round to the 8 samples that were positively diagnosed as *P. ramorum* in the first PCR round. While a precise quantification was not attempted, the PCR diagnostic was extremely more reliable than standard culturing techniques when analyzing leaf material. In the case of wood the technique was extremely successful, with a 53 percent increase in success (based on 79 samples), compared to standard culturing techniques.

Diagnosis from 51 oozing sap samples from cankers was highly successful (57 percent), while standard culturing of the same sap yielded only one positive isolation. This result suggests that while DNA diagnosis is extremely sensitive, it may not always indicate the presence of infectious propagules. Seasonal variability in the success of PCR diagnosis from oozing sap is suggested by our preliminary data (not shown). It appears that both culturing and PCR identification are more successful during the cooler and wetter months than in the summer time. Positive identification of *P. ramorum* from ooze may represent an excellent way to diagnose the disease. PCR amplifications were also positively performed from water and soil samples.

To our knowledge, this is the first time the study of a new fungal disease has been aided by DNA-based technology from its discovery. Molecular techniques were pivotal in providing rapid evidence of a connection between the American and European isolates of *P. ramorum*, in identifying plant material from species other than oaks as potential hosts of the disease (e.g., rhododendrons and other ornamentals), in broadening our understanding of the host range and of the biology and epidemiology of the disease, and finally in providing us with an invaluable tool that complements and improves the standard diagnosis technique based on live culturing of the pathogen.

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Population Diversity and Evidence of Introgression Among the Black Oaks of California[1]

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Abstract

The black oaks of California include 4 tree species (California black oak, coast live oak, Shreve oak, interior live oak) that are known to hybridize. Complex patterns of population variation within each species are likely to result from these hybrid combinations and from subsequent introgressions. We have been studying population variation using biochemical and molecular markers and report results from the former here. Diversity is much greater in interior live oak and in Shreve oak than in either of the other two species, and is least in coast live oak. Shreve oak has not received complete acceptance as a valid species, and is considered as synonymous with interior live oak by many ecologists. However, our biochemical data provided a marker that was present in all populations identified as Shreve oak from the central coast, and was extremely rare in populations of interior live oak from the Cascade and Sierra Nevada mountains. This marker occurred at intermediate frequencies in many populations from north western California that were tentatively assigned to interior live oak. We suggest that these two species are recently derived from a common ancestor and that interspecific barriers to fertilization have not yet become complete. Discriminant function analysis on the full biochemical data set suggested a complex pattern of introgression including coast live oak, interior live oak and Shreve oak in these north coastal populations. These studies of population variation help us to understand the genetic architecture of the black oaks of California and may provide valuable information in the search for resistance to sudden oak death (SOD).

Introduction

Four members of the black oak group (Lobatae) are native to California; coast live oak (*Quercus agrifolia*), interior live oak (*Q. wislizenii*), Shreve oak (*Q. parvula* var. *shreveii*) and California black oak (*Q. kelloggii*). Of these, the first three are evergreen oaks and the last is deciduous. All four species occur along the California coast and interior live oak and California black oak are also naturally distributed in the Sierra Nevada and Cascade mountains. In 1995 a disease was reported affecting tanoak (*Lithocarpus densiflorus*), that was subsequently attributed to a strain of *Phytophora* (Garbelotto and others 2001). This sudden oak death (SOD) disease is now reaching epidemic levels on tanoak, coast live oak and black oak (McPherson and others 2000), and has also been reported on Shreve oak and other unrelated

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species. The species being affected by this new disease are typical components of the coastal woodland vegetation of California. If the disease continues to spread, the impact on biodiversity could be catastrophic with potential loss of genetic diversity and of species. Several approaches are necessary in the attempt to control future spread of the disease, including the search for genetic resistance among the host species. Preliminary inoculation studies suggest that natural variation in resistance to SOD may exist in coast live oak (D. Rizzo, personal communication). With this in mind, the research reported here explores genetic architecture in the natural range of these species. Understanding levels of genetic variation and its partition within and among populations may be very helpful in developing a program aimed at identifying resistant genotypes, for setting guidelines for seed collection zones and for gene conservation.

In general, oaks, that are long-lived, outcrossed, wind pollinated species, are expected to exhibit a genetic architecture in which most variation is within rather than between populations (Hamrick and Godt 1989). Indeed, this has been the pattern observed for most species of oak that have been studied (Manos and Fairbrothers 1987, Guttman and Weigt 1988, Schnable and Hamrick 1990, Kremer and Petit 1993, Muller-Starck and others 1993). Little is known of the genetic variation among and within populations of the four California black oak species reported on here, but, as in most oak species, interspecific hybridization may be an important source of variation. Our earlier ecological genetic data suggested differentiation of central coast populations of coast live oak from those north of Cloverdale and south of Ojai (Dodd and others 1993a, 1997), which we attributed to possible introgression with Shreve oak in central California (Dodd and others 1993b, 1994, 1997). Recently, our molecular data have shown genetic similarity between interior live oak, Shreve oak and coast live oak, suggesting their close phylogenetic relationship (Kashani and Dodd 2002; Kashani, in press). We should therefore also expect hybridization to occur readily between Shreve oak and interior live oak. Indeed, the distributional limits of these two species in the Coast Ranges are unclear. It was therefore one of the objectives of this work to elucidate the taxonomic status of populations from the northern Coast Ranges that we attribute to the interior live oak complex.

For this work we have used biochemical markers (cuticular hydrocarbons) that have proven highly effective in identifying Shreve oak (Dodd and others 1997). Variation in cuticular hydrocarbon profiles is under strong genetic control, as shown by genetic studies of crop plants (Bianchi 1987, Jenks and others 1992) and by heritability estimates in coniferous species (Dodd and A. Rafii 2000) and in Mediterranean oaks.[4]

Methods

Foliage was collected from 29 populations of interior live oak and Shreve oak (referred to as the interior live oak complex hereafter) and from 27 populations of coast live oak. Sampling of the interior live oak complex was designed to include central California coast populations ascribed to Shreve oak, Sierra Nevada populations of interior live oak and a geographic series of populations connecting these two groups that approximately formed an inverted U around the northern Central Valley. Sampling of coast live oak was from throughout its range in the

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[4] Unpublished data on file, University of California at Berkeley, California.

northern and southern Coast Ranges, extending into Baja California. In addition 5 populations of California black oak were sampled from the Coast Ranges and the Sierra Nevada.

Mature foliage was collected at the end of the season from an average of 10 widely spaced trees per population. Only mature foliage from adult trees was sampled to avoid developmental and seasonal changes in cuticular lipid composition. The cuticular waxes were extracted by washing leaves in *n*-hexane for 3 minutes. The hydrocarbon fraction of the cuticular lipid extract was separated from other wax constituents by filtering the extract through a column packed with 0.5 g of 70-230 mesh silica gel. The hydrocarbon extract was analyzed on an HT-5 (0.25 mm internal diameter; 25 m length) capillary column in a Varian 3400 gas chromatograph. Alkanes were identified by comparing retention times with those of commercial standards. Chromatographic peak areas of identified compounds were expressed as a percentage of the total alkane extract.

Results

A homologous series of long chain alkanes ranging from 21 to 33 carbons was detected, with odd chain alkanes with carbon chain lengths from 25 to 33 predominating *(table 1)*. For all species, nonoacosane was the dominant alkane in the cuticular hydrocarbon mixture.

Table 1—*Mean percentage composition of cuticular hydrocarbons. Standard errors in parentheses. Major discriminating hydrocarbons shown in boldface.*

Alkane	Interior live oak	Shreve oak	Coast live oak	California black oak
C_{21} Heneicosane	0.16 (0.01)	1.90 (0.40)	trace	trace
C_{22} Docosane	trace	3.04 (0.64)	trace	0.21 (0.03)
C_{23} Tricosane	0.17 (0.03)	0.14 (0.02)	0.04 (0.003)	0.54 (0.08)
C_{24} Tetracosane	0.34 (0.04)	0.23 (0.03)	0.05 (0.004)	0.67 (0.10)
C_{25} Pentacosane	1.30 (0.09)	0.64 (0.08)	0.52 (0.03)	1.18 (0.13)
C_{26} Hexacosane	1.52 (0.08)	0.73 (0.07)	0.29 (0.02)	0.97 (0.07)
C_{27} Heptacosane	7.71 (0.31)	3.97 (0.41)	3.51 (0.12)	**14.40 (0.69)**
C_{28} Octacosane	2.84 (0.09)	2.68 (0.14)	2.11 (0.06)	2.14 (0.10)
C_{29} Nonacosane	77.02 (0.85)	49.52 (2.29)	**88.10 (0.35)**	78.60 (1.08)
C_{30} Triacontane	1.69 (0.14)	2.37 (0.12)	1.41 (0.04)	0.30 (0.04)
C_{31} Hentriacontane	7.02 (0.81)	**32.08 (1.97)**	3.90 (0.29)	0.85 (0.15)
C_{32} Dotriacontane	0.11 (0.02)	0.73 (0.07)	0.03 (0.004)	0.01 (0.004)
C_{33} Tritriacontane	0.12 (0.02)	1.96 (0.33)	0.05 (0.01)	0.03 (0.01)

Species Differences

California black oak was characterized by relatively high levels of heptacosane and low levels of hentriacontane, and coast live oak by the dominance of nonacosane *(table 1)*. The cuticular hydrocarbon profile of Shreve oak was the most distinctive, including very high levels of hentriacontane and greater than trace amounts of the very short chain alkanes, heneicosane and docosane.

Since the proportion of hentriacontane present in the cuticular wax profile appeared to be a good marker for separating the Shreve oak from interior live oak, it was tested as a possible indicator of hybridization between these two species. A frequency plot of percentage composition of hentriacontane for all individuals of interior live oak and Shreve oak suggested a trimodal distribution, in which individuals could be classified as low (0-10 percent of total hydrocarbons), medium (11-36 percent) or high (39-60 percent) chemotypes. The frequencies of these 3 chemotypes in all populations of the interior live oak complex are plotted *(fig. 1)*. With the exception of one population from Brickyard Road (Pop 23), all Sierran populations were composed entirely of individuals with low levels of hentriacontane. Populations from central coastal California were composed mostly of individuals with medium, or high levels of hentriacontane. North coastal populations varied in proportions of low, medium and high chemotypes, but only the medium and low chemotypes were present in northern populations (populations 16 and 17) connecting the Coast Ranges with the Cascade/Sierran distribution.

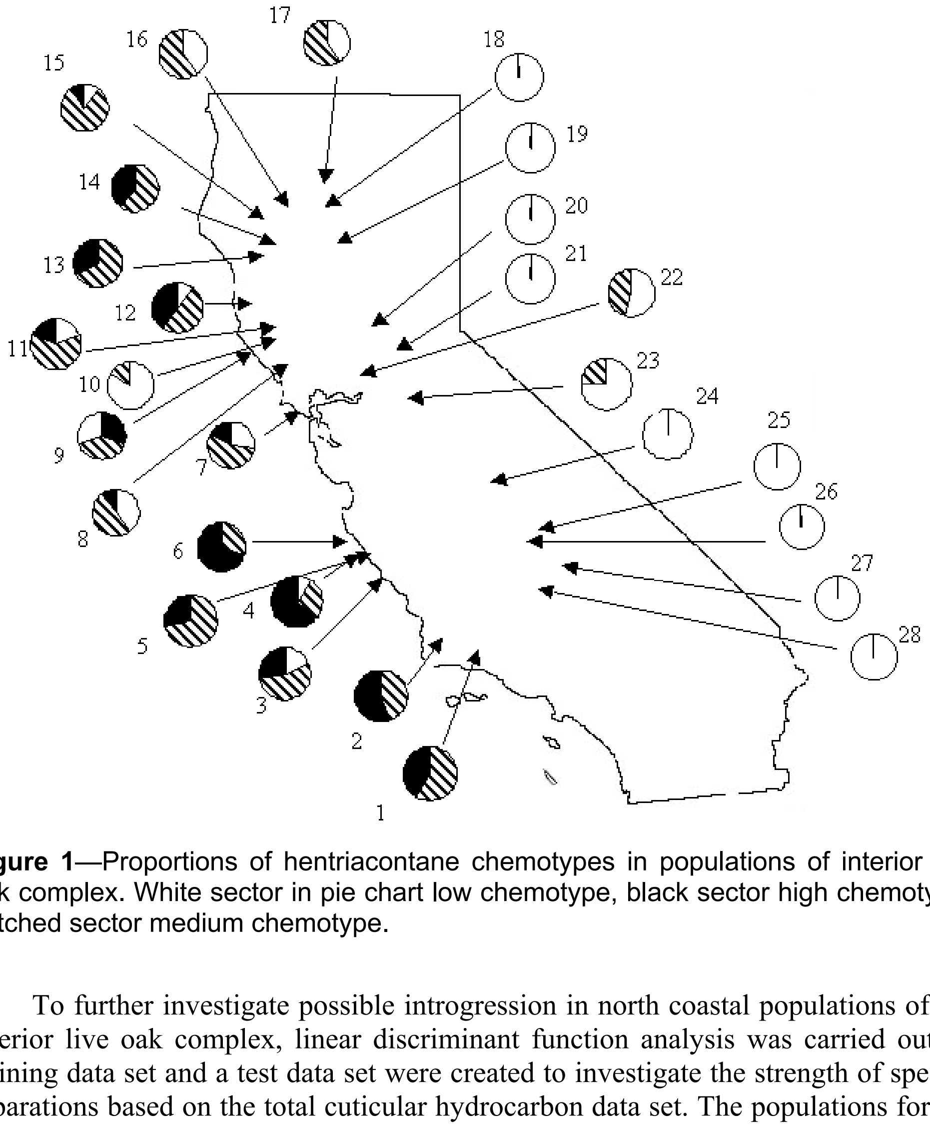

Figure 1—Proportions of hentriacontane chemotypes in populations of interior live oak complex. White sector in pie chart low chemotype, black sector high chemotype, hatched sector medium chemotype.

To further investigate possible introgression in north coastal populations of the interior live oak complex, linear discriminant function analysis was carried out. A training data set and a test data set were created to investigate the strength of species separations based on the total cuticular hydrocarbon data set. The populations for the training data set included all non-hybrid populations of coast live oak and of

California black oak, as these species are highly distinctive morphologically, and Sierran populations of interior live oak and central coast populations of Shreve oak. Remaining populations of the interior live oak complex, mainly from the northern Coastal ranges were included in the test data set. The training data set was used to derive discriminant functions that best separated the species and the test data set was used to ascribe individuals of uncertain affinity to species, based on the derived discriminant functions. The training data set produced a good separation of species with an overall error rate of 8.2 percent *(table 2)*. Classification error rates were 2.3 percent and 6.1 percent respectively for coast live oak and California black oak, whereas interior live oak and Shreve oak both had error rates of about 12 percent.

Table 2—*Percentage classification to species from discriminant function analysis.*

Field identification	**Pct of individuals classified into species by discriminant function classification on training data set**			
	Coast live oak	Cal black oak	Shreve oak	Interior live oak
Coast live oak	97.7	0.4	1.5	0.4
Cal. Black oak	4.1	93.9	0	2.0
Shreve oak	6.0	0	88.0	6.0
Interior live oak	7.6	3.5	1.4	87.5
	Pct of individuals classified into species by test data set			
Interior live oak	21.6	0	44.1	34.3

All individuals of the test data set were assigned to the interior live oak complex in the field, partly because morphological separation of interior live oak and Shreve oak was not certain, and partly because distinction of these two taxa in the northern Coast Ranges was being investigated. Only 34 percent of individuals from the test data set were assigned to interior live oak *(table 2)*. Twenty two percent were assigned to coast live oak and 44 percent were assigned to Shreve oak. No individuals from the test data set were assigned to California black oak. The proportion of individuals in populations assigned to the three species are shown in a distribution map *(fig. 2)*. Individuals from the northernmost populations at Douglas City and Whiskeytown were all assigned to interior live oak. Remaining populations included varying proportions of individuals assigned to coast live oak, interior live oak and Shreve oak.

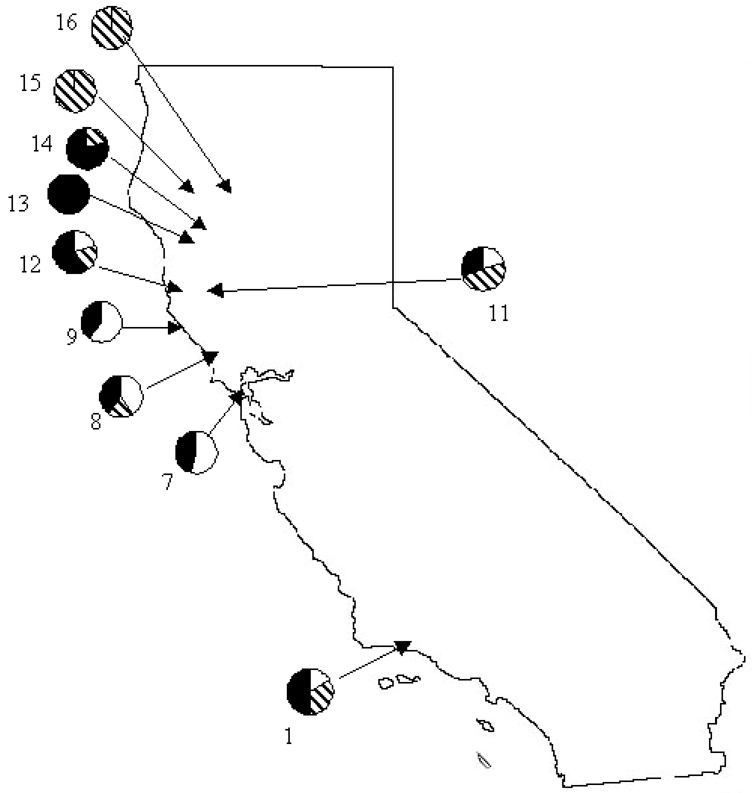

Figure 2—Proportions of individuals in populations of the interior live oak complex from the Coast ranges attributed to species from discriminant function analysis. White sector in pie charts coast live oak, black sector Shreve oak, hatched sector interior live oak.

Genetic Diversity

Plots of frequency distributions of percentage composition were skewed, with a strong tendency towards tri-modality for 5 of the cuticular alkanes. This type of frequency distribution can be explained by the presence of three chemotypes for each of the 5 alkanes; low, medium and high chemotypes. The frequencies of the 3 chemotypes by species and by population within species were calculated, and the resulting chemotype frequencies were used to estimate chemotypic diversity using Shannon's diversity index:

$$D = -\Sigma \log_3 p_i(p_i)$$

where p_i is the proportion of individuals with each of the i chemotypes.

Chemotypic diversity was least in coast live oak and greatest in interior live oak and Shreve oak *(table 3)*. The unassigned populations were no more diverse, on average, than either of the two latter species. Average diversity estimated over all individuals, ignoring population structure, is a measure of total diversity for the species. For coast live oak, this estimate did not differ from the average of populations. However, in the remaining species total average diversity was much greater than average of populations, suggesting much greater within population variation in these species.

Table 3—*Shannon's diversity index for populations of oak species. Numbers in parentheses refer to populations numbered on figures 1 and 2.*

Coast live oak				**Cal black oak**		**Interior live oak**		**Shreve oak**		**Unassigned populations**	
Population	D		D	Population	D	Population	D	Population	D	Population	D
Cloverdale	0.04	Lompoc	0.04	Redding	0.12	Kern R. (25)	0.10	Purisima (2)	0.09	Cachuma (1)	0.10
Franz Valley	0.02	Ojai	0.02	Legget	0.08	Wofford Hts. (28)	0.08	Plaskett Cr. (3)	0.15	Mt. Tamalpais (7)	0.11
Crane Park	0.04	Valencia	0.02	Round Vlly.	0.06	Kernville (27)	0.02	Palo Colorado 1 (4)	0.17	Geysers (8)	0.14
Point Reyes	0.06	Cleveland 1	0.02	Petaluma	0.11	Cal. Hot Spr. (26)	0.11	Palo Colorado 2 (5)	0.19	Gualala (9)	0.16
Pacheco Pk.	0.08	Cleveland 2	0.02	San Pablo	0.05	Mariposa (24)	0.13	Big Sur (6)	0.13	Orrs Spr. Rd. (12)	0.13
Pacheco Pass	0.08	Fallbrook	0.02			Brickyard (23)	0.12			Lower Lake (10)	0.06
Fremont Pk.	0.08	Peutz Valley	0.03			Roseville (22)	0.13			Clearlake (11)	0.16
San Juan Rd.	0.09	San Ysabella	0.04			American R., Cool (21)	0.17			Farley (13)	0.05
Parkfield	0.10	Vallecitos (BC)	0.02			Hwy 70 (20)	0.17			Round Valley (14)	0.06
San Miguel	0.02	San Antonio (BC)	0.02			Red Bluff (19)	0.19			Douglas City (15)	0.18
Paso Robles	0.04	La Mission (BC)	0.02			Redding (18)	0.07			Whiskeytown (16)	0.13
Blk. Mountain	0.03	Santo Thomas (BC)	0.07			Lake Shasta (17)	0.11				
Cambria	0.05	San Pedro Martir (BC)	0.05								
Population mean			**0.05**		**0.08**		**0.12**		**0.14**		**0.12**
All individuals			**0.05**		**0.21**		**0.22**		**0.22**		**0.20**

Within Species Population Structure

Canonical discriminant analysis was carried out on the matrix of cuticular hydrocarbon composition for coast live oak and for the interior live oak complex. Population mean scores of the first two canonical vectors are plotted *(figs. 3* and *4)*.

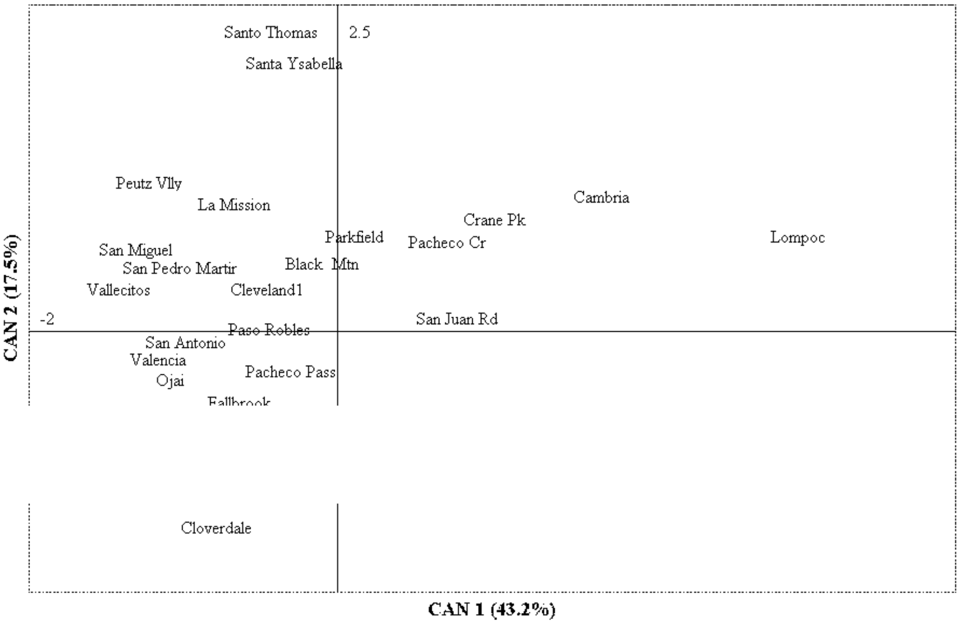

Figure 3—Plot of the first two canonical discriminant vectors of cuticular hydrocarbon composition among populations of coast live oak.

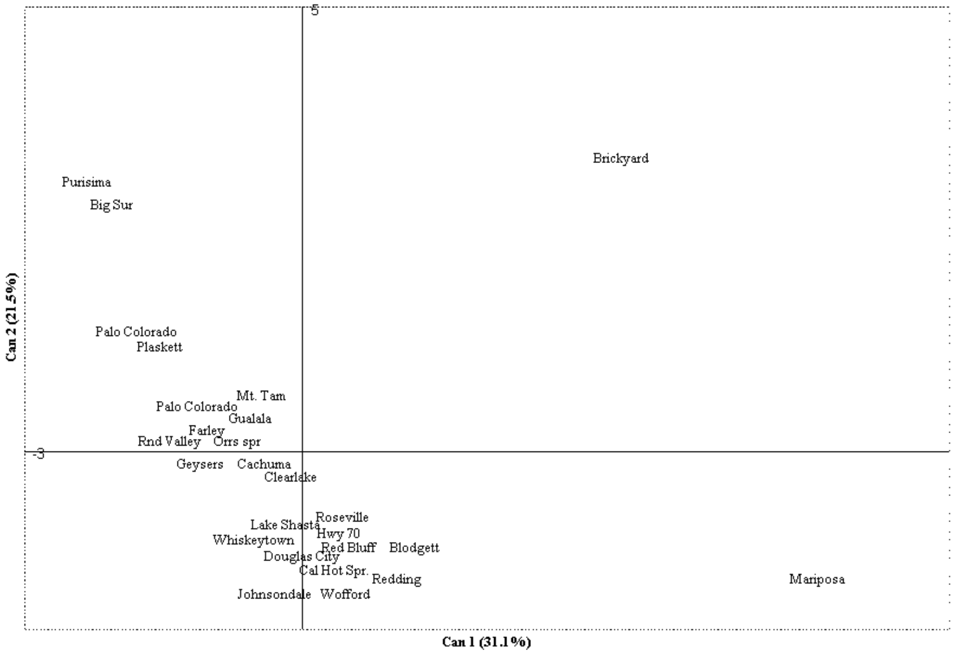

Figure 4—Plot of the first two canonical discriminant vectors of cuticular hydrocarbon composition among populations of the interior live oak complex.

For coast live oak, the first four canonical vectors were significant at the $P<0.0001$ level and together accounted for 79 percent of the variance. The plot of the first two vectors showed a geographic trend, in which southernmost populations were on the negative side of the origin along the first canonical vector *(fig. 3)*. With the exception of Cloverdale and Paso Robles, central and northern populations were close to the origin or on the positive side along the first vector. Within these two main geographic groups, no clear geographic, or ecological trend was evident.

The first 8 vectors were significant at $P<0.0001$ for the interior live oak complex, of which the first 4 explained 75 percent of the variance. The plot of the first two vectors showed a trend from populations of Shreve oak in the upper left quadrant through unassigned populations close to the origin and populations of interior live oak in the lower half of the plot, either close to the origin or in the lower right quadrant *(fig. 4)*. Three populations assigned to interior live oak were well separated from all others. These three populations from Brickyard Road, Lower Lake and Mariposa, were mixed with California black oak and their cuticular hydrocarbon profiles showed some affinities with this species.

Discussion

Morphological differentiation of Shreve oak and interior live oak has proven difficult, with the result that the distributions of these two species in the California Coast Ranges is inconclusive. According to Tucker (1993), the former species is found in the Southern Coast Ranges and in the San Francisco Bay Area, but Shreve oak is still not fully accepted by the scientific community. Whereas, molecular markers have not been successful in separating these two taxa (Kashani and Dodd 2002), cuticular lipid composition appears to provide a remarkably powerful method for their distinction. Unusually high levels of hentriacontane appear to be unique for Shreve oak, among the four black oak species native to California. In pure populations of interior live oak, coast live oak and California black oak, only the low hentriacontane chemotype is present.

Hybridization among oak species is common, and is reported to occur among these four black oak species (Tucker 1980). In our earlier work (Dodd and others 1997), we reported on a low frequency of medium hentriacontane chemotypes in central coastal populations of coast live oak, and concluded that this was due to introgression of Shreve oak genes. Our more extensive analyses of coastal and interior populations of the interior live oak complex support this earlier interpretation of chemotypic variation, and suggest that cuticular biochemistry is a sensitive indicator of introgressive gene flow. Among our unassigned populations of this group, discriminant function analysis on the full cuticular hydrocarbon data, placed some individuals to coast live oak. Populations with individuals assigned to coast live oak fell entirely within the distributional range of this species, providing indirect support for the sensitivity of this method. All individuals were identified morphologically as belonging to the interior live oak complex, and no morphologically identified hybrids were included in the analysis. Results of the discriminant analysis therefore suggest that introgressive gene flow is important in these populations and introgression of coast live oak genes appeared to be greatest in the coastal populations at Mt. Tamalpais and at Gualala. Remaining individuals in each of these unassigned populations were attributed to Shreve oak or to interior live oak and never to California black oak, even though hybrids among all four species are known to occur.

In the unassigned populations, individuals attributed to Shreve oak exceeded those attributed to interior live oak, except in the extreme north at Douglas City and Whiskeytown. In these two latter populations all individuals were attributed to interior live oak. The canonical discriminant function plot and the map of hentriacontane chemotypes strongly suggest a transition in the Cascade Mountains from a coastal to a Sierran form of interior live oak. Should coastal forms all be treated as Shreve oak? We suggest that central coast populations at low elevations, typically occupying redwood forest should be treated as Shreve oak. This region may extend as far north as the San Francisco Bay. However, it seems likely that Shreve oak and interior live oak are poorly differentiated, probably from a recent ancestor and that in the northern Coast Ranges, a complex mix of the two taxa, along with hybrids and introgressants, exists, probably varying in proportions according to ecological preferences. The Shreve oak form gradually falls out eastward to the Sierra Nevada, probably as summer drought limits its success. Among the four species studied chemotypic diversity was greatest in interior live oak and in Shreve oak, which might be expected if these two species were relatively poorly differentiated and were forming hybrid complexes.

Sudden oak death has been reported on coast live oak, California black oak and on Shreve oak, but not yet on interior live oak. It is not yet clear whether lack of reports of infection on the latter species are due to its occurrence on drier sites, due to misidentification or due to genetic resistance. The present work points out the biosystematic complexity of these black oak populations, which needs to be understood in attempting to find resistant genotypes.

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Evaluation of Stem Water Potential and Other Tree and Stand Variables as Risk Factors for *Phytophthora ramorum* Canker Development in Coast Live Oak[1]

Tedmund J. Swiecki[2] and Elizabeth Bernhardt[2]

Abstract

We conducted a case-control study to examine the role of water stress and various other factors on the development of *Phytophthora ramorum* cankers in symptomatic (case) and symptomless (control) coast live oak (*Quercus agrifolia*) and tanoak (*Lithocarpus densiflorus*). Midday stem water potential (SWP) in *Q. agrifolia* subject trees ranged from –0.25 to –3.1 megapascals (MPa). SWP was higher (indicating lower water stress) in cases than controls. Other variables significantly associated with disease in *Q. agrifolia* included tree canopy dieback, the amount of the canopy shaded by other trees, and the density of California bay in the plot. Cases were also significantly associated with counts of other plot trees with early *P. ramorum* canker symptoms, indicating that spatial aggregation of diseased trees occurs on the scale of the plot area (0.02 hectare). For *Q. agrifolia*, the incidence of decline and death related to *P. ramorum* in case plots was almost equal to rates of decline and recent mortality due to other agents. For *L. densiflorus*, decline and mortality related to *P. ramorum* was far more common than decline and mortality due to other agents.

Introduction

Phytophthora ramorum has been associated with elevated levels of mortality in tanoak (*Lithocarpus densiflorus*), coast live oak (*Quercus agrifolia*), and California black oak (*Q. kelloggii*) trees in a number of California coastal counties over the past few years (Garbelotto and others 2001, Rizzo and others 2002b). Early symptoms of the disease, which is commonly referred to as "sudden oak death," consist of bark cankers which typically produce a brown exudate. The sapwood-decaying fungus *Hypoxylon thouarsianum*, oak bark beetles (*Pseudopityophthorus* spp.), and ambrosia beetles (*Monarthrum* spp.) are commonly associated with *P. ramorum*-infected trees in later stages of decline. These agents also attack declining trees or branches that are not infected with *P. ramorum*

Very little was known about the epidemiology of this disease at the time this study was initiated. Water stress had been considered as a possible risk factor for disease development because affected trees are commonly found in highly competitive situations. Water stress occurring either before or after infection has been

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[1] An abbreviated version of this paper was presented at the Fifth Symposium on Oak Woodlands: Oaks in California's Changing Landscape, October 22-25, 2001, San Diego, California.

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shown to increase the susceptibility of various plants to *Phytophthora* spp. (Sinclair and others 1987) and is also a predisposing factor for *Hypoxylon* infection (Sinclair and others 1987) and beetle attack.

To examine the role of water stress and various site and stand attributes on the development of *P. ramorum* bole cankers, we conducted a case-control study in areas where the disease was common. Case-control studies are designed to examine how past (retrospective) factors are related to the current health of individuals. In this study, we investigated whether water stress and various other tree and stand factors are risk factors for the early phase of the disease, i.e., the bleeding bark cankers that are associated with *P. ramorum* infections. Current tree and stand conditions were used as indicators of past conditions at the site.

Midday stem water potential (McCutchan and Shackel 1992) can be considered an indicator of preexisting water stress levels if *P. ramorum* infection does not substantially affect water transport or tree water potential. *P. ramorum* cankers affect the bark but generally do not affect substantial amounts of xylem tissue (Garbelotto and others 2001, Rizzo and others 2002b), at least in trees in early stages of disease that we selected as cases. Therefore, we assumed that case trees were not likely to exhibit changes in stem water potential brought about by infection with *P. ramorum*.

Due to limitations of time and funding, we concentrated our efforts on one host species, coast live oak. For comparative purposes, we also collected a limited amount of data on tanoak. This study addresses only the trunk cankers caused by *P. ramorum* on coast live oak, black oak, and tanoak. Foliar infections on tanoak*,* California bay *(Umbellularia californica),* and various hosts were not known at the time that this research was conducted

Methods

In this study, cases were defined as live trees with evident *P. ramorum* cankers but lacking fruiting of *H. thouarsianum* and evidence of beetle boring on the bole that is typical of *P. ramorum*-infected trees in late stages of decline. Hence, cases are characterized as having early disease symptoms only. Controls were trees lacking evident *P. ramorum* cankers, although it is possible that some controls could have been infected but still asymptomatic trees. Cases and controls were sampled within areas where the disease syndrome is prevalent. This reduces the likelihood that controls simply represent trees that have not been exposed to any *P. ramorum* inoculum, although this possibility cannot be ruled out for all controls.

Study Site Selection

During September 2000, we established plots and collected data at 12 study locations *(table 1)*. Study sites were selected on the basis of appropriate vegetation type*,* the presence of case and control coast live oak or tanoak trees in the study area, and absence of recent disturbances that might affect tree health.

Table 1—*Locations of plots and host species studied.*

Location number	Location	County	Number of plots	Subject tree species
1	Marin Municipal Water District (MMWD) watershed - Azalea Hill area	Marin	12	coast live oak
2	MMWD-Pumpkin Ridge south	Marin	16	coast live oak
3	MMWD-Pumpkin Ridge north	Marin	11	coast live oak
4	MMWD-Phoenix Lake area	Marin	11	coast live oak
5	China Camp SP - Miwok Meadows area	Marin	16	coast live oak
6	China Camp SP - SE Buckeye Point area	Marin	12	coast live oak
7	Woodacre (Private land)	Marin	12	coast live oak
8	Lucas Valley (Private land)	Marin	12	coast live oak
9	Muir Woods NM / Mt. Tamalpias SP	Marin	10	tanoak
10	Wall Road (Private land)	Napa	13	coast live oak
11	Marin County Open Space land, Novato	Marin	13	coast live oak
12	Jack London SP	Sonoma	12	tanoak

Plot Selection

At each study location, we collected data on 10 to 16 circular 8 m radius (0.02 ha) fixed area plots, each of which was centered around a subject case or control tree. The number of plots per location was limited by the time constraints associated with stem water potential measurements and terrain. At each location, we entered into the stand, selected a random bearing and proceeded along that bearing to search for the nearest case or control tree. We attempted to space adjacent tree-centered plots approximately 25 m apart, but actual interplot spacing varied with vegetation and terrain. Distances between two adjacent plots ranged from 16.1 to 48.8 m (average 26.1 m). Plots at the various locations were distributed over areas ranging between about 0.75 and 1.6 ha. We attempted to alternate case and control plots, but if the alternate subject tree type did not exist within a 4 to 8 m search radius of the target point, the same type was repeated. We collected data on 75 control and 53 case plots for coast live oak, and 13 control and 9 case plots for tanoak. Overall, controls outnumber cases because trees showing early *P. ramorum* symptoms were often difficult to locate when following the sampling pattern we used.

Stem Water Potential Determinations

We collected midday stem water potential (SWP) readings on the center subject tree in each plot during the 2 hour peak midday period (1:00-3:00 P.M. PDT) following methods outlined by Shackel (2000). On each tree, two leaves or shoot tips with several leaves were sealed inside clear plastic bags and overbagged with larger opaque reflective plastic bags. We selected leaves that arose directly from the trunk, main branches near the trunk, or basal sprouts. Bags were left in place for 2 or more hours to allow leaf water potential to equilibrate to that of the subtending stem. Each leaf or shoot tip was then excised and placed into the pressure chamber while still sealed in the clear plastic bag. One or two SWP determinations were made per tree. In general, two valid SWP measurements from a single tree were within 0.05 to 0.1

megapascals (MPa) of each other. SWP measurements were made with a pump-up pressure chamber (PMS Instrument Co., Corvallis OR) fitted with a 4 inch diameter 40 bar (0.4 MPa) gauge with 1percent accuracy.

To estimate vapor pressure deficit (VPD) during the period that SWP readings were made, we recorded the minimum and maximum temperature and relative humidity values using a portable electronic thermohygrometer (Mannix TH Pen, model PTH8708). The thermohygrometer was placed in a ventilated shelter mounted on a mast and was positioned near the upper portion of the tree canopy layer during the observation period. VPD was calculated from the average of the recorded minimum and maximum temperature and relative humidity values.

Additional Tree and Plot Variables

In addition to SWP determinations, subject trees were rated for origin class (seed or coppice); stem count; stem diameter(s) at 137 cm diameter at breast height (DBH); and amount of crown exposure to overhead sunlight (using 0-6 scale described below). Counts of *P. ramorum* cankers were estimated from bleeding areas and girdling by *P. ramorum* cankers was rated by estimating the percent bole circumference girdled as if all cankered areas were projected on same cross section. The horizontal extent of cankers was estimated from the distribution of bleeding areas, alterations in bark appearance, and some limited chipping of outer bark to expose canker margins. We also assessed overall (chronic) canopy thinning (none, slight, definite), the presence of epicormic branches (none, few, numerous), and recent canopy dieback (0-6 scale below). Although assessment of actual levels of decay in standing trees is problematic, we rated decay impact (none, low, moderate, high) by assessing the probability that existing decay would have a significant negative impact on tree health or survival. The assessment of decay impact was based on the type(s) of decay present, location of decay within the tree, and the estimated extent of decay as rated by a trained observer. Additional details of the tree health rating methods are presented in Swiecki and Bernhardt (2001).

Plot variables recorded included plot slope and aspect; total basal area; tree counts by species; plot canopy cover; woody understory cover; disease status or recent mortality (estimated within the preceding 10 years) of other coast live oak, black oak, and tanoak trees in the plot; counts of regeneration of these 3 host species; and the presence of other pathogens of these species. Coast live oak, black oak, and tanoak trees other than the center subject tree are referred to as plot trees in this paper.

Other than basal area, which was assessed using a 5 m^2/ha BAF reticle, plot-related variables were assessed on an 8 m radius fixed-area plot centered at the subject tree. The measured variables were also used to calculate a number of additional variables for various analyses. We used plot slope, aspect, elevation, and latitude data to calculate the total annual insolation (solar radiation) that the plot would receive in the absence of shading from vegetation or nearby landforms. Insolation was calculated using a program developed by Dr. Tom Rumsey (Department of Biological and Agricultural Engineering, University of California, Davis) based on the Hottel estimation model (Duffie and Beckman 1991)

We used the following arcsine-transformed percentage scale for most ocular estimates of percentages: 0= not seen, 1= less than 2.5 percent, 2= 2.5 percent to 19 percent, 3= 20 percent to 49 percent, 4= 50 percent to 79 percent, 5= 80 percent to 97.4 percent, 6= more than 97.5 percent. *P. ramorum* girdling rank was derived by grouping percent girdling estimates into the following classes: 0= 0 percent, 1= 1 percent to 19 percent, 2= 20 percent to 39 percent, 3= 40 percent to 59 percent, 4= >59 percent.

Statistical Analyses

We used JMP® statistical software version 4.0.4 (SAS Inc., Cary NC) for data analysis.[3] Unless otherwise indicated, effects or differences are referred to as significant if $P \leq 0.05$. We fitted logistic regression models to the data to examine the effects of factors on the binary disease outcome (subject tree is diseased, i.e., a case). Although we constructed logistic regression models for both tanoak and coast live oak, only the latter models are reported here.

We screened possible predictor variables using univariate logistic regressions, examined correlations between predictor variables, and checked predictor variable distributions to ensure that models were not overly influenced by a few outlying observations. We developed multivariate models using a stepwise procedure. Factors were generally considered for entry into the multivariate models if odds ratios from univariate models were significant at $P \leq 0.10$. The significance level of each factor reported in the final models should be interpreted as if it were the last factor added to the model.

We used linear regression, analysis of variance, and analysis of covariance to test for associations between continuous outcomes (e.g., SWP) and continuous or categorical predictor variables. We also used analysis of variance (F-tests) or t-tests to test whether mean levels of continuous variables differed between cases and controls.

Results

Disease Levels within Plots

Overall densities of coast live oak, black oak, and tanoak did not differ between plots in which the subject tree was a case (case plots) and plots in which the subject tree was a control (control plots). However, plot trees with *P. ramorum* cankers were more numerous in case plots than control plots *(table 2)*. In a two-way analysis of variance on percent *P. ramorum* infection of plot trees (arcsine transformed data), plot type (case/control) was significant at $P=0.01$, species was significant at $P=0.058$, and the interaction term was not significant.

In contrast, rates of decline and death of coast live oak, black oak, and tanoak due to agents other than *P. ramorum (table 2)* did not differ significantly between case and control plots. For coast live oak in case plots, the percentage of trees declining or recently killed by other agents (33 percent) was not significantly different than the total percentage of trees affected by *P. ramorum* (25 percent). For tanoak, the percentage of trees affected by *P. ramorum* in case plots (56 percent) was far in excess of the background decline and mortality associated with other agents (6

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[3] Mention of trade names or products is for information only and does not imply endorsement by the U.S. Department of Agriculture.

percent). Levels of *P. ramorum*-related mortality were also much higher in tanoak than in live oak *(table 2)*.

Table 2—*Incidence of symptomatic trees and recent (10 year) tree mortality associated with* P. ramorum *or other agents in study plots. Totals exclude symptoms on the plot subject tree.*

Plot type	Species	Number of trees	Due to *P. ramorum*			Due to other agents	
			Early symptoms	Late symptoms	Dead	Severe decline	Dead
Control	Live oak	321	7.2 pct	4.0 pct	2.8 pct	17.4 pct	6.9 pct
	Tanoak	93	9.7 pct	2.2 pct	14.0 pct	4.3 pct	5.4 pct
	Black oak	7	14.3 pct	14.3 pct	0 pct	28.6 pct	0 pct
Case	Live oak	251	14.7 pct	4.8 pct	6.0 pct	27.1 pct	6.0 pct
	Tanoak	54	29.6 pct	3.7 pct	22.2 pct	5.6 pct	0 pct
	Black oak	11	18.2 pct	0 pct	0 pct	27.3 pct	36.4 pct

Stem Water Potential

SWP measurements varied widely among subject trees within locations. We developed an analysis of covariance model for coast live oak that accounted for about half of the variation in SWP *(table 3)*. SWP was negatively correlated with insolation and the percent of the tree canopy exposed to direct overhead sunlight (sky-exposed canopy). These results indicate that subject tree SWP is higher (i.e., water stress is lower) in plots that receive lower amounts of solar radiation (e.g., north-facing slopes) and in trees with heavily shaded canopies. SWP was also negatively correlated with VPD overall, but further analysis showed that the correlation was significant only among trees with more than 50 percent sky-exposed canopy (interaction term in *table 3*).

Table 3—*Analysis of covariance model for midday stem water potential (MPa) of coast live oak.*

Source	DF	F Ratio	Prob>F	Adjusted R^2	N
Overall model	6	21.67	<0.0001	0.517	117

Model terms	DF	F Ratio	Prob>F	Parameter estimate
Vapor pressure deficit (KPa)	1	5.06	0.0026	-0.101
Sky-exposed canopy	1	37.45	<0.0001	-0.172
Annual insolation (MJ/m^2)	1	10.33	0.0017	-0.000153
P. ramorum girdling rank	1	7.59	0.0069	0.0930
Decay impact rating	1	6.24	0.0140	0.120
Interaction: Sky-exposed canopy >50 pct [true] × (VPD-daily mean VPD)	1	5.58	0.0199	-0.108
Intercept				0.0920

SWP was also correlated with two tree health variables *(table 3)*. Variables describing *P. ramorum* presence or severity (canker count, percent girdling, girdling rank, case/control) were positively correlated with SWP. Girdling rank was the most highly significant of these variables and was included in the final model *(table 3)*.

Water stress, as measured by SWP, was lower in cases than controls and the severity of *P. ramorum* girdling generally increased as water stress decreased. This result is consistent with our assumption that early stages of *P. ramorum* infection seen in cases would not adversely affect SWP. The positive association between disease and high SWP suggests that, after adjusting for other factors in the model, trees located in relatively moist areas are at higher risk for disease than those located in drier sites

SWP was also positively correlated with decay impact ratings in the subject tree *(table 3)*. Hence, the development of wood decay in *Q. agrifolia* also appears to be favored by moist sites. However, other tree condition variables, including canopy thinning and dieback, were not correlated with SWP. This suggests that SWP is not elevated in diseased trees simply due to a reduction in the amount of transpiring leaf area.

Because SWP readings were taken on different days, we needed to adjust the observed SWP readings to account for the effect of VPD in order to create valid SWP variables for use in logistic regression models. Two variables successfully removed the effect of VPD on SWP. Of these the difference from $\mathrm{SWP}_{\mathrm{max}}$ (maximum SWP from all trees on a given date – tree SWP) was more highly significant in multivariate models (discussed below) although the likelihood ratio for this variable was significant only at $P=0.0533$ in univariate logistic regression models for the case outcome.

Other Variables Associated with Occurrence of P. ramorum *Canker*

For both coast live oak and tanoak, the risk of *P. ramorum* canker in the subject tree was elevated if other symptomatic trees were present in the plot (univariate logistic regression, likelihood ratio $P=0.0254$). For coast live oak plots, the risk of early disease symptoms in a subject tree increased with the number of other plot trees showing early *P. ramorum* canker symptoms, i.e., bleeding but no evidence of beetle attack or *H. thouarsianum* fruiting (likelihood ratio $P=0.0145$). However, the number of plot trees with late *P. ramorum* canker symptoms and/or dead trees with *P. ramorum* canker symptoms were not significant predictors of disease in the subject tree. Furthermore, the number of plot trees showing late disease symptoms was not correlated with the number of plot trees showing early disease symptoms. Similar patterns were observed in tanoak plots

Evidence of bark and/or ambrosia beetle damage and fruiting bodies (stromata) of *H. thouarsianum* were found in 63 percent of coast live oak plots and 36 percent of tanoak plots. For live oak, the presence of beetle damage and *H. thouarsianum* fruiting within the plot were correlated, and the presence of these agents was associated with disease in the subject tree, the number of plot trees with *P. ramorum* cankers, and the number of declining and dead host trees due to causes other than *P. ramorum.*

No other disease or damage agents that we recorded were significantly associated with cases. Of the other agents that are associated with oak mortality, canker rots (typically caused by *Inonotus* spp.) were the most common. Canker rot symptoms and/or fruiting bodies were observed in 63 percent of coast live oak and 18 percent of tanoak plots. Fruiting bodies of *Phellinus* spp., *Ganoderma* spp., and *Laetiporus sulphureus* were observed in about 11 percent, 2 percent, and 1 percent respectively of the coast live oak plots. Particularly in live oak, *P. ramorum* cankers sometimes occurred in trees that were declining due to canker rot infection or other agents that are not normally associated with *P. ramorum*-related mortality.

Other subject tree factors that were positively associated with disease in univariate models included the canopy dieback rating (likelihood ratio P=0.0410), sky-exposed canopy rating (likelihood ratio P=0.0012), and number of stems (likelihood ratio P=0.0061). Among plot variables, only the count of California bay trees in the plot showed a significant positive association with disease in the subject tree (likelihood ratio P=0.0024).

Multivariate Logistic Regression Models for P. ramorum *Canker in Coast Live Oak*

Many of the individual predictor variables discussed above are correlated or interrelated in various ways. We constructed multivariate logistic regression models to gain insight into the relative strength of various predictor variables and the degree to which predictor variables can be substituted for each other. In general, highly collinear variables cannot be fitted into the same model. Given several related and highly correlated variables, we selected the variable that improved overall model fit the best. Inclusion of a factor in a model does not necessarily imply a causal relationship between the factor and the outcome. Predictor variables included in a model may in fact be outcomes that are influenced by the same underlying (and possibly unmeasured) factors that influence disease risk.

We first fitted a multivariate model that included all significant predictors. We then eliminated two predictors in this model (California bay density, cross-sectional area of largest stem) whose significance in the model was dependent on a few extremely high outliers in their data distributions. This model *(table 4)* correctly classified 77 percent of the subject trees as cases or controls, using P(outcome)>0.5 as the criterion for predicting either outcome (case or control). The model was more successful at predicting controls (87 percent correctly classified) than cases (65 percent correctly classified).

This model is moderately successful at predicting disease in subject trees, but requires information on the incidence of *P. ramorum* cankers on plot trees, SWP of the subject tree, and canopy dieback rating. Such a model would not be of much use for predicting disease risk in an unsurveyed stand because of the detailed site and tree observations are required. Therefore, we also constructed a reduced model *(table 4)* that omits these more data-intensive variables. The reduced model correctly classified 71 percent of the subject trees as cases or controls, and correctly assigned 75 percent of the cases and 70 percent of the controls. Note that California bay density was significant in this model even with high outliers for this variable omitted. Bay density and SWP are correlated to a high degree, so typically only one or the other could be included in a given multivariate model. The reduced model suggests that multistemmed coast live oaks with high amounts of sky exposure that are surrounded by high numbers of California bay trees may be at increased risk of *P. ramorum* canker.

Table 4—*Multivariate logistic regression model parameter estimates for the binary disease outcome (case) for coast live oak.*

	Full model[1]		Reduced model[2]	
Predictor variables	**Likelihood Ratio Prob>χ^2**	**Odds ratio (95 pct confidence interval)**	**Likelihood Ratio Prob>χ^2**	**Odds ratio (95 pct confidence interval)**
More than 2 stems [true]	0.0009	14.6 (2.77 - 124)	0.0011	11.5 (2.48 - 87.2)
Sky-exposed canopy >50 pct [true]	<0.0001	10.6 (3.67 - 36.0)	0.0001	5.69 (2.30 - 15.90
Difference from SWP_{max} (MPa)	0.0057	0.0430 (0.00347 - 0.415)		
Canopy dieback >20 pct [true]	0.0062	3.66 (1.43 - 10.2)		
Count of trees with early *P. ramorum* symptoms	0.0239	8.96 (1.34 - 65.8)		
Count of California bay trees			0.0223	8.42 (1.35 - 63.4)

[1] Overall model likelihood ratio P<0.0001, n=127 (one record omitted due to missing data for one variable).

[2] Overall model likelihood ratio P<0.0001, n=125. Three plots with outlying high California bay counts (28-32 bay/plot) were omitted from the analysis. Overall model significance and significance of this factor are increased if the outliers are included.

Discussion

The primary objective of this study was to examine the relationship between water stress and *P. ramorum* infection. We found a significant positive association between disease and high SWP, which does not support our original hypothesis that disease might be more common or severe in water-stressed trees. Instead, the data are consistent with the hypothesis that trees located in relatively moist areas are at higher risk for disease than those located in drier sites.

One or more of several possible explanations could explain why disease risk may be elevated for trees in moist sites. Because *Phytophthora* spp. are highly dependent on wet conditions for disease development, environmental conditions associated with moist sites could be especially favorable for the pathogen. For example, prolonged dew periods or extended periods of soil saturation might occur in these areas and could favor sporangium production, zoospore motility and germination, and/or infection. High soil moisture might also alter host susceptibility. For instance, coast live oaks growing in wetter sites might experience relatively rapid trunk growth, possibly increasing the amount of growth cracks in the bark or otherwise rendering the bark more susceptible to infection.

Furthermore, it is now clear that *P. ramorum* causes foliar infections on many species (Rizzo and others 2002b) and such infections may be important sources of inoculum. Therefore, the association between disease and moist sites may be related to the presence of more foliar *P. ramorum* hosts and/or greater levels of foliar disease in such sites. Our analyses indicated that the density of California bay within the plot showed a significant positive association with disease. *P. ramorum* can cause foliar infections on California bay (Rizzo and others 2002a) although this was not known at the time we originally reported this association (Swiecki and Bernhardt 2001).

Because California bay is more common in relatively moist or mesic sites within coast live oak woodlands (Griffin and Critchfield 1976), we cannot cleanly separate the possible effects of high site moisture per se and inoculum production on

California bay leaves. The interaction between these factors may actually be the basis of the increased disease risk associated with these two predictors. In addition, because California bay produces relatively dense evergreen shade, the presence of high bay populations might also help create favorable microclimate conditions for disease development, for instance by slowing the rate at which stems dry. Further investigation will be needed to explore the how these interrelated factors influence disease risk.

P. ramorum-infected trees are more common in case plots than control plots *(table 2)* and disease risk in the subject tree is elevated if other plot trees are also symptomatic *(table 4)*. From these results, we infer that infected trees are spatially aggregated, at least on the scale of the plot size used in this study (0.02 ha). However, the lack of correlation between late disease symptoms in plot trees and early disease symptoms in the subject tree or other plot trees leads us to conclude that bole cankers present within a plot (i.e., within an 8 m radius) may not be an important source of inoculum for the initiation of new cankers.

The overall fit of our two multivariate models *(table 4)* was reasonably good despite the limited number of predictors variable included. The magnitudes of the effects in the models are quite substantial, although the confidence intervals for the odds ratios are large due to the limited sample size. We believe that these factors or closely related factors should be considered in further attempts to model *P. ramorum* disease risk in coast live oak. Nonetheless, our models do not include variables that may be important in disease development, such as the genetic resistance level of individual trees. In addition, the data set used to develop the model may include a number of control trees that are infected but had not yet developed visible symptoms. A follow-up survey of these trees has recently been completed, and information about the change in disease status of control trees should allow us to improve our disease risk models.

Areas sampled in this study were limited to those where *P. ramorum* canker was common. Therefore disease levels in these plots may be greater than would be expected overall across affected areas. Furthermore, because plots were selected based on the occurrence of a case or control tree and were not random, they do not provide unbiased estimates of disease levels in the sampled stands. Nonetheless, the relative levels of disease and mortality associated with *P. ramorum* and other agents are worth noting.

P. ramorum has doubled the mortality of coast live oak in case plots, whereas mortality in control plots has been increased by about 50 percent to date. The effect on tanoak is even more pronounced, because this species is both more susceptible to *P. ramorum* and exhibits relatively low rates of mortality due to other causes *(table 2)*. Overall tanoak mortality rates we observed (about 22 percent in case plots and 19 percent in control plots) are well above the rates reported by Hunter (1997). In a stand in Mendocino County, he recorded 6 percent mortality among tanoaks <20 cm DBH and 9 percent mortality among tanoaks >20 cm DBH over a 14 year period (1981-1995). *P. ramorum* canker thus has the potential to substantially alter the composition of affected stands.

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Monitoring Sudden Oak Death in California Using High-resolution Imagery[1]

Nina Maggi Kelly[2]

Abstract

The Sudden Oak Death (SOD) epidemic in California is alarming for those living with, and adjacent to, the complex of oak and tanoak woodland that exist in patches along the coast. Monitoring SOD occurrence and spread is an on-going necessity. Remote sensing methods have proved to be successful in mapping and monitoring forest health and distribution when a sufficiently small ground resolution is used. In this project, digital high-resolution (1-m) ADAR imagery was analyzed for an area including and surrounding China Camp State Park in Marin County, California in the spring of 2000 and 2001. This paper reports on two analyses: First, the individual frame data from 2000 was mosaiced and classified to reveal 5,340 dead and dying trees in the area including and surrounding China Camp State Park. Second, a smaller subset of the study area was used to perform a Normalized Difference Vegetation Index (NDVI) image differencing and thresholding routine between 2001 and 2000. This change detection showed trees that were misclassified in the 2000 image, as well as newly dead trees. For the smaller study area (303 ha) there were 1,091 dead or dying trees in March 2000, and 317 trees that died in the 13 months that followed. Trees that died between March 2000 and May 2001 were located between 5 and 52 m away from existing dead trees.

Introduction

The newly discovered pathogen *P. ramorum* has been killing hundreds of thousands of trees in California since it was first reported in 1995 (Svihra 1999). Tree species hosts of this new disease include but are not limited to two valuable oak species: coast live oak (*Quercus agrifolia*) and black oak (*Q. kelloggii*). The seemingly rapid decline of the symptomatic trees has led to the disease complex name Sudden Oak Death (SOD) (McPherson and others 2000). As of October 2001, the disease has been officially confirmed in 10 coastal counties of California *(fig. 1),* and hosts for the disease exist in several more counties. (It was also detected on 40 acres in southern Oregon and is known to cause leafspots and twig dieback on rhododendron in Germany and the Netherlands.) Marin County is one of the "hot-spots" for SOD with areas displaying dramatic dieback of tanoaks, coast live oaks and black oaks. Establishing the baseline conditions of Sudden Oak Death in California in 2000, and monitoring its spread through 2-5 years is a critical need for management of this new disease (more detailed information about the pathogen will

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be provided in the accompanying papers in this volume and elsewhere (i.e., Garbelotto and others 2001, McPherson and others 2000, Svihra 1999).

According to best knowledge, the pathogen appears to enter through the bark of susceptible oak trees, and cause rapid canker development that leads to girdling and dramatic and often rapid death of the tree (Garbelotto and others 2001). This pattern of disease progression facilitates the use of remote sensing methods for disease analysis. Remote sensing has been used to map and monitor the location and effects of forest disease (Macomber and Woodcock 1994), and in disease studies to map habitat of invertebrate disease vectors (Hay and others 1997) using imagery of multiple spatial resolutions. This paper describes the analysis of high-resolution imagery (1-m) to map and monitor SOD in an especially hard-hit area in Marin County, California. Results from an earlier classification of high-resolution imagery were combined with a change detection routine to refine the earlier classification in order to discern both trees that were mis-classified in the earlier analysis, as well as trees that have died in the period between March 2000 and May 2001. The study area includes area surrounding China Camp State Park in Marin County. An analysis of the distance between recently dead trees and the closest dead tree was also calculated to determine if there was an indication of tree-to-tree infection.

Background

Study Area

The study area for this project is a forested peninsula on the east side of Marin County (see *fig. 1* for general location and *fig. 2* for specific map of the study area).

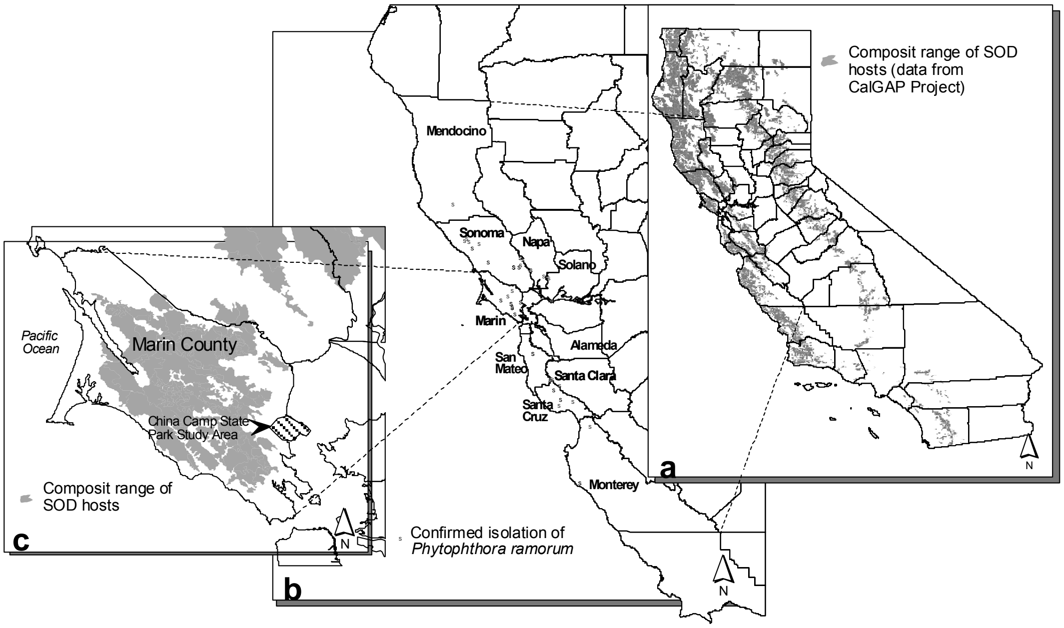

Figure 1—Sudden Oak Death in California: a) California with the distribution of susceptible host species; b) the counties with confirmed SOD, and locations of positive samples; and c) Marin County, showing the study area and the possible range of host species within the County.

The area has moderate to steep topography, with elevations ranging from sea level at San Francisco Bay to over 300 m. Open space here is managed in the northwest by Marin County Open Space, and in the west and south by California State Parks. The area currently managed as China Camp State Park has an interesting land use history, it has been in the recent past an off-road motorcycle range, the location for a renaissance faire, and since 1977 it has been a state park. The forest stands there are near even-age stands, these hillsides were cleared for lumber in the early to mid-1800s. Coast live, black and valley oaks are abundant, and occur in mixed stands with mature madrone and bay trees providing habitat to a variety of wildlife, including deer, squirrels and numerous birds. All of these trees with the exception of valley oak are hosts for *Phytophthora ramorum*.

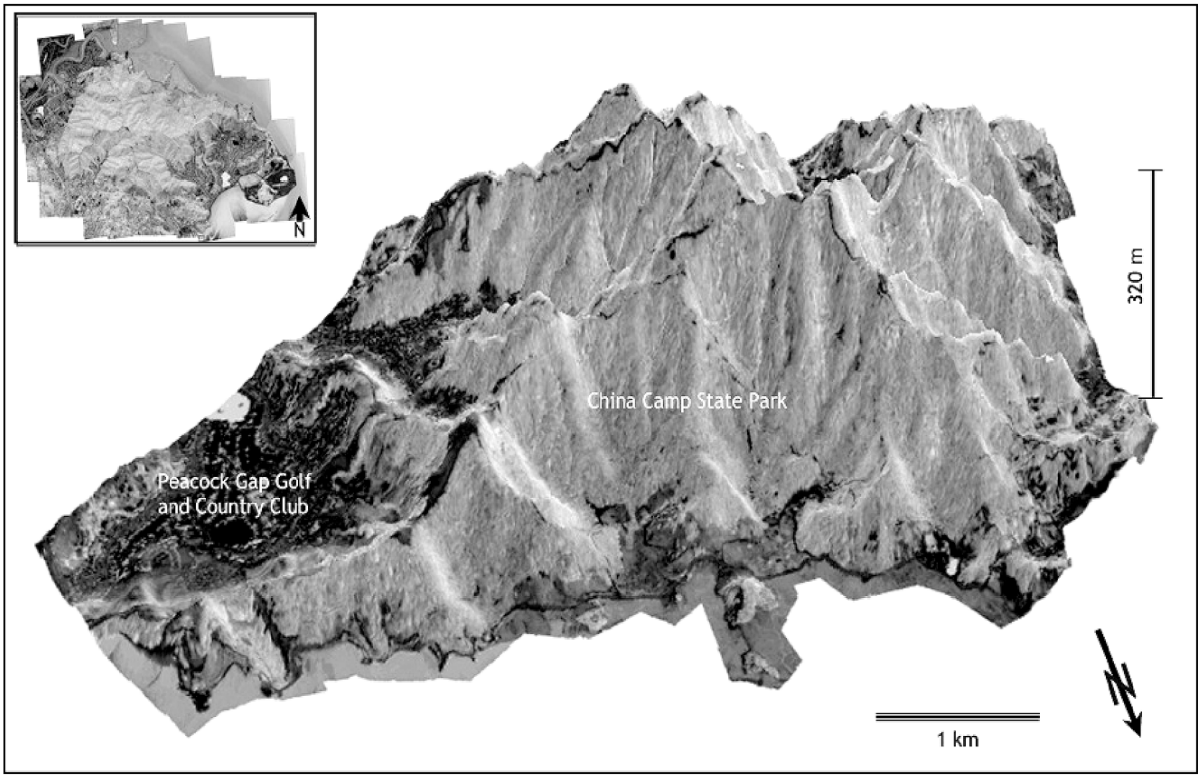

Figure 2—Mosaiced ADAR imagery of the area including and surrounding China Camp State Park in Marin County, California. The image is a false color composite draped over digital elevation model; healthy vegetation is shown in the lighter areas. The undraped mosaic appears in the upper left hand corner; north in this inset is towards the top.

Remote Sensing of Oak Death

The ability to locate and quantify change in an area can be a valuable asset to natural resource management. Change detection methods using digital remotely sensed data have utility in detecting specific disturbances (Kelly 2001a) and changes in landscape composition and structure (Green and others 1994, Lunetta and Elvidge 1998). The use of remote sensed data for monitoring forest health and forest inventories has a recent history (Franklin and others 2000, Macomber and Woodcock 1994, Pinder and McLeod 1999). With some notable exceptions (Boyer and others

1988, Everitt and others 1999, Gong and others 1999), much of this work has examined conifer stands. The pathology of this new disease affords an opportunity for continued development of techniques for remote sensing in hardwood forests. Specifically, the disease has three characteristics that make a monitoring approach that ties remote sensing with fieldwork ideal. First, as the trees with the disease die, in most cases the entire crown changes dramatically from healthy green to brown, and over a short time period. Second, after canopy change has occurred, the leaves can stay adhered to the branches for months giving trees a characteristic "freeze-dried" appearance. Third, in areas where SOD is advanced, the affected trees display spatial clumping, with diseased trees likely to be clustered together. This pattern can result in dramatic spectral reflectance changes across broad areas. In addition, the affected *Quercus* species make good targets for high-resolution imagery. For example, coast live oaks have a broad multi-stem canopy with leaves and a canopy structure that has evolved to maximize contact with sunlight (Pavlik and others 1991). In the study area most affected trees are over 100 years old, and form the dominant overstory canopy. High-resolution imagery can assist in several feature extraction problems. In the ADAR imagery used in this project it is possible to differentiate between some hardwood species (Bay trees and oaks are distinct in this figure), discern healthy appearing and dying oaks (the healthy oaks are dark red in this image, and the dying trees have a blueish grey tone), and clearly map man-made features such as roads and trails *(fig. 3).*

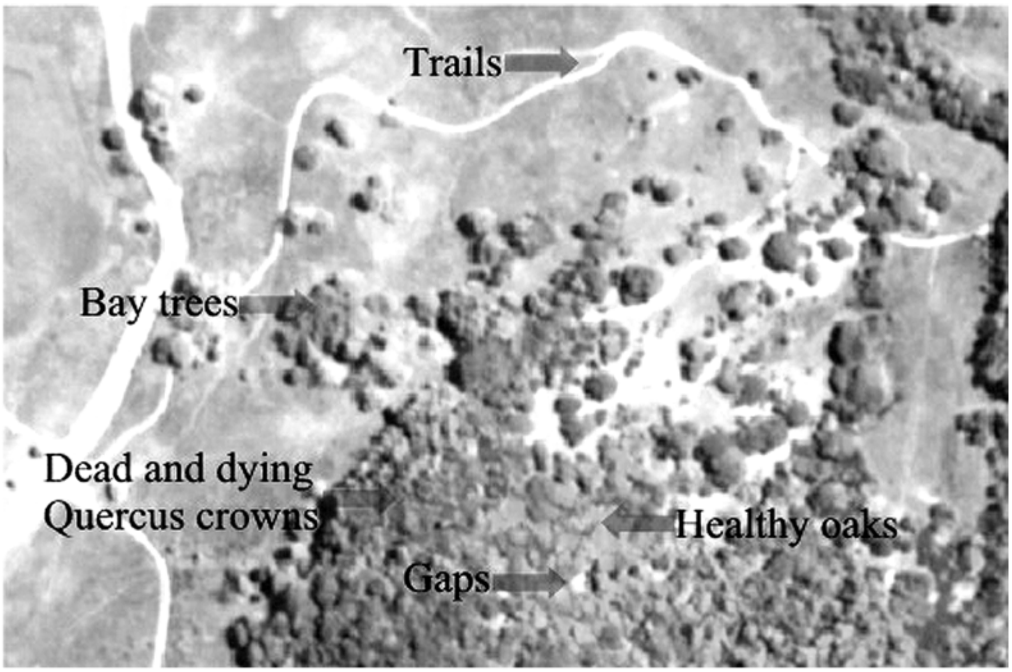

Figure 3—An area in China Camp State Park that has SOD as it was imaged using the ADAR system. The image shows spectral difference from targets. Healthy appearing oaks and California bay trees can be distinguished from dead and dying crowns of oaks.

Methods

Imagery Acquisition and Preprocessing

Digital imagery (ADAR 5500) was acquired for the China Camp study area in 2000 and 2001 with an ADAR 5500 imaging system that was comprised of a SN4, 20mm lens with four mounted cameras (Spectral Bands: Blue: 450-550 nm; Green: 520-610 nm; Red: 610-700 nm; Near Infrared (NIR): 780-920 nm), flown at an average aircraft altitude of 2,205 m. We contracted with a private company (Positive Systems Inc. from Montana) to perform the imagery acquisition and registration. The average ground spatial resolution of the images is 1-meter. Each 1,000 x 1,500 m frame was captured with standard 35 percent end and 35 percent side-lap. Imagery was acquired on March 30, 2000 and May 5, 2001. These near anniversary dates were chosen to maximize the springtime canopy cover changes associated with SOD, and to minimize misclassification caused by early color change of California buckeye, a summer drought deciduous tree that can, when seen from a distance can appear similar to SOD affected trees. Weather precluded image capture in 2000 in April.

The frames from 2000 were mosaiced and geo-referenced using a 6-inch resolution digital ortho-photograph of the entire county provided by Marin Municipal Water District. The contractor provided the image registration using in-house DIME software. Registration accuracy was 0.305 m throughout the scene. The 2000 mosaic was clipped to remove urban and non-wooded areas. *Figure 2* shows the clipped imagery draped over a digital elevation model.

Classification of 2000 Imagery

Once mosaiced, a standard set of topographic correction and spectral enhancements were performed using Erdas Imagine software (Erdas 1999). First, a Lambertian topographic correction was applied to the imagery (Jensen 2000). A variety of spectral (i.e., PCA, Kauth Thomas Tassled Cap, and Normalized Difference Vegetation Index (NDVI)) and spatial (texture) enhancements were evaluated to determine their utility in discerning dead and dying trees from healthy green foliage. These enhancements have been used to map vegetation using remotely sensed data. Many were developed for Thematic Mapper data (Crist 1985, Yuan and others 1998), but as the spectral resolution of ADAR is almost identical to TM in bands 1-4, these enhancements can be used here. NDVI has proven to be a useful in pre-classification enhancement because it is least affected by topographic changes (Lyon and others 1998). Both visual inspections of the study area and field data acquired from a series of plots designed to measure symptom progression provided ground truth to validate the results of the enhancements. The NDVI provided a very useful transformation, with dead and dying crowns visible, as did the 3rd Principal Component (from a standard PCA analysis), and all three indices from a Tassled Cap analysis (greenness, wetness, brightness). A new layer stack that combined the five enhancements mentioned above was created for subsequent unsupervised classification. A simple visible to NIR ratio ((band1 + band2 + band3) / band4) was successful in pulling out trails from background forest, but was too highly correlated with the NDVI to include in the stack.

The 5 enhancements bands were classified using the Erdas Imagine default isodata unsupervised classification cluster algorithm. The isodata clustering routine uses minimum distance formula to form clusters (Erdas 1999). The process yielded 25 classes, 5 of which were clearly dead and dying crowns or bare ground. Confusion between dead and dying crowns and bare areas was eliminated by disregarding patches that were too large or that had shapes uncharacteristic of a tree crown. Field visits were also made to explain the resulting confusion between bare ground and dead and dying trees. Finally, each patch of dead or dying tree was visually inspected in the imagery to determine the likelihood that it was a tree, and not a bare area. A centroid routine was run to determine the centers of all dead and dying crowns, and the number and location of all dead and dying trees.

Accuracy assessment was performed by selecting from the classified imagery 100 randomly located dead and dying trees in the area of China Camp State Park and verifying their status in the field. The fact that the accuracy assessment was performed almost a year after the imagery was flown did not create a problem. Trees that were dead and dying in spring 2000 remained dead in spring 2001 (or showed signs of having been recently removed). Trees that were healthy in spring 2000 and dying in spring 2001 could be assumed to be green in 2000, as the canopy transformation associated with SOD usually takes weeks, not months. This accuracy assessment was not designed to determine spectral class accuracy, but accuracy of a binary image (dead and dying/healthy), so no error matrix was generated.

Image-to-Image Registration and Radiometric Normalization

Initially, the 2001 frames were registered to the 2000 mosaic with a substantially larger root mean squared error (RMSE) (4.5 m), which was unacceptable for a change detection routine. This larger error was due to the extreme terrain in the area. To correct for the problem, the 2000 and 2001 images were clipped to create a smaller study area that had sufficient visible ground control, and less overall terrain, to perform a more accurate image-to-image rectification process for the purposes of this paper. Image to image registration was performed on the clipped portion of the 2001 mosaic, using the clipped portion of the 2000 image as the control. 65 control points were used with a second-order polynomial transformation yielding an overall RMSE of 1.587m.

Radiometric enhancement deals with the individual digital brightness values (BVs) of the pixels in the image. The ranges of BV in both time periods should be similar before change detection routines are used. Radiometric normalization was performed by use of normalization targets. According to this normalization method, a simple linear regression can be performed using the BVs of targets in the base image against the BVs of the targets in the other images to determine radiometric correction values. Appropriate target reflectors are discussed in several places including (Dobson and others 1995). Targets chosen for this project included two spectrally invariant ponds, a parking lot, and a road surface. A simple linear regression model was computed for the BVs of the target reflectors in 2000 and the BVs of the targets in 2001 for bands 3 and 4. The slope and y-intercept of the regression equations were the used to normalize the 2001 image to the 2000 base image: the y intercept provides an additive component that corrects for the difference in atmospheric radiance, and the slope provides a multiplicative term that corrects for the difference in detector calibration, sun angle, Earth-to-Sun distance, atmospheric attenuation and phase angle differences between dates (Kelly 1996).

Change Detection

In the case of SOD in Marin County, there are four states of change that are of interest:

- Case #1: Healthy to healthy: indicating that there is no change in tree condition;
- Case #2: Healthy to dead or dying: indicating trees that have died in the interim between spring 2000 and spring 2001;
- Case #3: Dead to healthy: indicating trees that were classified incorrectly in 2000 as dead or dying, but that are most likely deciduous oaks;
- Case #4: Dead to dead; those dead in 2000 that remain dead in 2001, or dead trees that have been removed in March 2000.

NDVI subtraction and thresholding facilitated quantification of the latter three of these cases. While several methods exist, NDVI subtraction and thresholding is one of the more useful yet least complicated of all change detection routines (Lunetta 1998, Lyon and others 1998, Yuan and others 1998). For this project, the NDVI from 2001 was subtracted from the NDVI from the 2000, yielding a pixel-by-pixel change in spectral reflectance associated with healthy vegetation. The resulting image was thresholded (thresholds were 10 percent at the extreme negative end and 15 percent extreme positive end of the NDVI difference) to show areas of greatest change by comparing the resultant change image with several trees whose change from 2000 to 2001 was known.

This method resulted in many spurious or incorrect areas of false change that had to be screened out. There were two kinds of change to examine here: first, those pixels that indicated NDVI had decreased significantly from 2000 to 2001 (Case #2: new death or tree removal), and second, those pixels that indicated NDVI had increased (Case #3: misclassification as dead of a deciduous, but healthy oak). To remove those pixels that indicated new death but that were obviously erroneous (too large to be a tree, obvious slivers caused by mis-registration, and change over bare areas), clumps of pixels were sorted by size and shape (using shape index "K"—a modified perimeter to area ratio described in Kelly [2001b] and Davis [1986]), and those too large, too small or too elongated to be a tree crown were removed. Following this, all remaining clumps were visually inspected to determine if they denoted newly dead trees. A centroid routine was performed on the remaining clumps to locate the tree center, and these points were added to the dead and dying tree layer. In addition, the distance from these newly dead trees to previously dead trees was calculated. To determine which of the third kind of change—NDVI increase—corresponded to a tree classified in 2000, the point location of all dead and dying trees from the 2000 classification routine were buffered to a distance of 2 m. This buffer coverage was overlaid on a vectorized coverage of NDVI change to determine intersection between the features. All clumps of pixels that showed an increase in NDVI that were within 2m of a dead and dying tree center were called Case #3 pixels. The corresponding point from the dead and dying tree layer was deleted.

Results

Imagery Classification

The classified imagery from 2000 yielded 5,340 dead and dying crowns in the area covered by the entire study area *(fig. 4).* This clipped imagery covers an area of 917 forested ha. Dead and dying crowns occur throughout the forested area, but visually show definite clustering patterns. The accuracy of this map product was field verified to be 92 percent. However, there was some confusion (reported below) between the deciduous oaks (primarily valley oaks) and dying trees in the 2000 imagery.

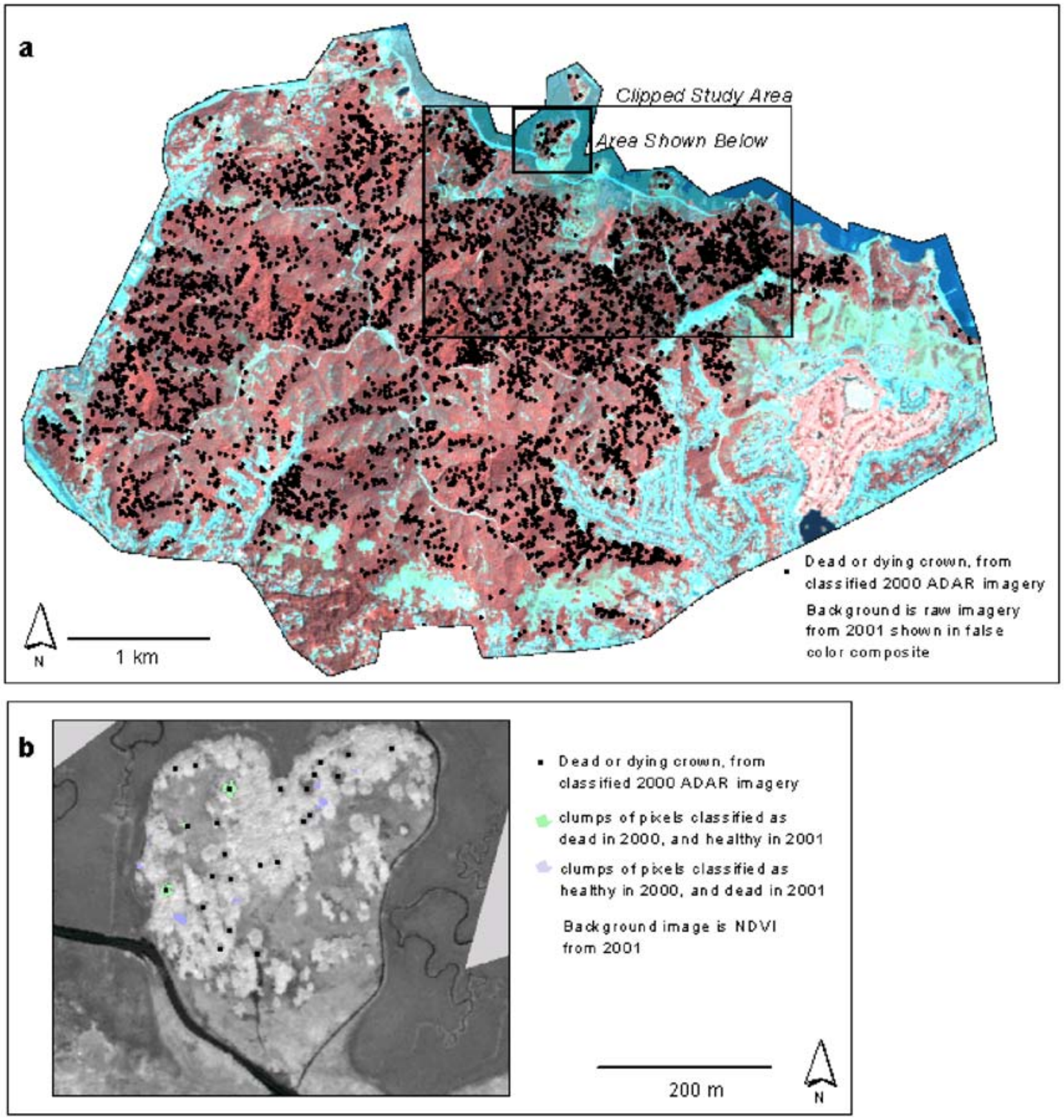

Figure 4—a) Map of dead trees in China Camp State Park area from classification of 2000 mosaiced ADAR imagery. There are 5,340 dead trees distributed throughout the area shown (1,708 ha, of which 917 ha is forested). b) Smaller subset of area used for change detection analysis showing highlighted change areas derived from a NDVI subtraction algorithm. This area highlights newly dead trees, as well as those deciduous oaks that were misclassified in the 2000 analysis.

Change Detection

Within the smaller subset of the study area (shown in *figure 4*) there were 1,523 dead and dying trees as calculated using the analysis of the 2000 imagery data. Of these, 432 trees showed significant increase in NDVI from 2000 to 2001, and were determined to be incorrectly classified. These trees are assumed to be deciduous oaks. This results in an error of commission in the analysis of 2000 imagery to be much higher than earlier reported: 28 percent. In addition, 317 tree crown areas showed significant decrease in NDVI, and were determined to have died in the 13 months between the two time periods.

The newly dead trees were not always close (< 10 m) to already dead trees. The minimum distance a newly dead tree was from an existing dead tree was 0.5 m, and the maximum distance was 52.9 m. The average distance was 17.6 m, and 114 trees are over 20 m from the closest existing dead tree.

Discussion

This research presents total numbers of dead and dying trees over two periods in time, and gives an estimate of the number of trees that have died in the interim. According to this work, the area including and surrounding China Camp State Park in Marin County, California (900+ ha of forested land) has on average about 6 dead and dying trees per ha. The seasonality of imagery acquisition is critical to the success of the classification. While in March 2000 the deciduous oaks had fully leafed out at the time of imaging, the leaves were immature and this negatively influenced the NIR reflectance. This resulted in several cases of misclassification (errors of commission) where deciduous oaks were identified as dead or dying trees. When the second set of images was acquired in May 2001, the deciduous oaks were leafed-out with mature, high reflective leaves. There is also classification confusion not related to seasonality. Spectral confusion exists between dead and dying crowns and small forest gaps, but this was corrected through selection of shape metrics, and field reconnaissance.

The image rectification process with ADAR imagery remains a challenge. ADAR is imaged in frames, and these are then combined and georectified into a continuous mosaic. This process is not trivial, and it can be very problematic. The registration between the 2000 and map base layer was good: 0.3 m. But the registration between the 2000 and 2001 imagery was not as good: 4.5 m. Therefore the registration parameters were recreated and the 2001 image reprojected to reduce the error.

From March 2000 to May 2001 many new trees appeared to have died. While numbers of dead trees, and general rates of dead trees per area are useful for management and public awareness of the disease, the methods described here do not yield other measurements important for understanding of SOD disease progression such as rates of infection and speed of death. Measurement of the rate of infection requires the calculation of the number of susceptible trees in the area, which is not a trivial task. Indeed, estimations of the number of crowns in a closed canopy forest from remotely sensed imagery remains a challenge. Estimation of the population of host species will be pursued in the future.

The broad range of distances from newly dead trees to their immediate dead neighbor confirms new results from research into the pathology of the complex. It is currently believed that oaks are a terminal host for this disease. Infection then will most likely not occur from tree to tree. As most of the newly dead trees occurred between 15-20 m away from the closest dead tree, and some as much as 50+ m away from the closest dead tree, this indicates the presence of alternate hosts between dead crowns. Research will continue to explore the spatial pattern of these alternate hosts.

These results should be interpreted cautiously. The methods outlined here measure only dead and dying overstory crowns and not infected trees. It has not been proven that this method can routinely map infected trees with green crowns (i.e. stressed individuals that have not gone through canopy color changes).

Conclusion

Four-band ADAR imagery is useful in mapping dead overstory trees in forest stands affected by Sudden Oak Death. The methods presented here are sufficient to determine the numbers of trees that are dead and dying in an area using high-resolution imagery, however, they require considerable field knowledge and operator time. It is possible that faster, more automated methods can be developed. Efforts continue to develop and test more automated classification and change detection methods and to refine the rectification results.

It is clear that China Camp State Park exhibits extensive overstory mortality. While we cannot assume that every tree that appears to be dead in the forest is a result of SOD, it seems likely that at least half of the trees are affected by the disease in areas where SOD is well established, such as China Camp. Background rates of oak mortality are not known in these areas, but one written estimate indicates a range from 2 percent to 50 percent (Sweicki and Bernhardt 2001). Clearly more research is needed in determining background oak mortality in this forest. Further field validation of the results will help determine both the accuracy of these maps, and assist in measuring rates of disease infection and progression.

From the initial spatial analysis of the dead crowns it appears that the mortality is not just intensifying areas of infection and remaining close to existing dead trees, but expanding into new areas of infection. These results will be examined further with more robust spatial analysis methods to determine disease spread pattern.

This work is in its initial phase. The disease is new to science, and as new techniques are being investigated for control and management of the disease, the monitoring techniques being developed here are also likely to evolve through the next 5 years as other sensors are evaluated, and new GIS modeling techniques are applied to the problem.

Acknowledgments

The author would like to thank Pat Robards, Ranger of China Camp State Park for description of the Park and surrounding area’s history, and for access to the Park. Initial support for this research came from the University of California’s Division of Agriculture and Natural Resources (DANR), and through DANR’s Monitoring Landscape Change Workgroup. The work was completed in association with the UC Berkeley Center for the Assessment of Forest and Environmental Resources (CAMFER). The paper was strengthened by comments by two reviewers.

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Phytophthora ramorum and Sudden Oak Death in California: IV. Preliminary Studies on Chemical Control[1]

Matteo Garbelotto,[2] David M. Rizzo,[3] and Lawrence Marais[4]

Abstract

Chemical applications may provide one means of control for *Phytophthora ramorum*, the cause of Sudden Oak Death (SOD). Such controls have been effective with other *Phytophthora* species in landscape and orchard situations. We have initiated laboratory and field studies to test the efficacy of a number of products previously reported to control *Phytophthora*. "In vitro" tests have determined that many of the standard chemical controls (e.g., metalaxyl, copper sulfate, phosphoric acid) are effective against *P. ramorum*. Field and green house studies include experiments to treat trees and saplings already infected with the pathogen as well as treatments to protect trees from infection. Application of chemicals has been by drench, injection, and topical application directly to the bark. Although preliminary results are positive, it should be pointed out that use of chemical controls will be limited to urban situations and specimen trees. It is unlikely that chemical controls will be of practical use in California wildland situations.

Introduction

The genus *Phytophthora* includes several plant pathogens, and chemical control of *Phytophthora spp*. is a common practice for agricultural crops (Erwin and Ribeiro 1996, Guest and others 1995). A wide array of compounds is commercially available, often with active ingredients and formulations that may be specific to one or a few species of the pathogen and to one type of application (e.g., foliar sprays vs. injections). Rate of active ingredient, time of application, phytotoxicity, and the potential for the rise of resistance to the chemicals in individuals of the pathogen, are all important considerations when planning a chemical application (Garbelotto and others 2001). In the case of natural ecosystems, the use of chemical control is, for obvious reasons, even more problematic. Nevertheless, chemical control may be an important tool in specific situations, for instance if trying to eradicate a pathogen from limited infestation foci. Chemical control can also be important as part of an integrated management approach, when trying to protect individual or small groups

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of trees. There are at least two known successful examples of chemical treatments of *Phytophthora* in forest ecosystems (Fernandez-Escobar and others 1999, Hardy 1999).

Phytophthora ramorum is a newly described species (Werres and others 2001), and the likely cause of a lethal disease of at least three species of California oaks (*Quercus* spp.), and tanoak (*Lithocarpus densiflora*) (Garbelotto and others 2001, Rizzo and others 2002). No information is available on the susceptibility of this pathogen to compounds used for the control of other *Phytophthora* species, and on the efficacy of chemical treatments in controlling the canker disease this pathogen causes.

In this paper, we describe the first series of “in vitro” tests aimed at determining the sensitivity of *P. ramorum* to several chemical compounds. We also describe an experiment on potted saplings in which chemical injections were used to control the growth of *P. ramorum*.

Materials and Methods

In Vitro Tests

Chemical compounds listed in *table 1* were used in these trials. For each compound, the 1X concentration was based on amounts recommended by the manufacturer for woody ornamentals or orchard trees. Each compound was tested at the following concentrations: 10X, 1X, 1:10X, 1:50X, 1:100X, 1:200X, 1:500X. Standard 10 percent V8 growth medium (Erwin and Ribeiro 1996) was amended with varying amounts of each compound, in order to obtain the concentrations listed above. V8 agar without any additions was used as a control treatment. Both the amended and unamended media were poured in 6 cm-diameter Petri dishes, and left to solidify overnight.

Table 1—*Chemical compounds and their concentrations that were used in tests for control of* Phytophthora ramorum.

Active ingredient (A. I.)	1X concentration (percent A.I.)
Metalaxyl	0.012
Phosetyl-Al	3.200
Phosphorous acid	2.000
Propiconazole	0.017
Copper Sulfate Pentahydrate	0.100

Three isolates of *P. ramorum* were employed: Pr-1 (coast live oak, Marin CO.), Pr-2 (tanoak, Marin CO.), and Pr-4 (tanoak, Marin CO.). Plugs from actively growing edges of colonies were then transferred at the center of each Petri dish. For each isolate and compound concentration, five (trial a) and three (trial b) replicates were performed, so that at a total of 15 (trial a) plates were used for each compound concentration tested.

Plates were inoculated and placed in an incubator at 22°C. Size of each colony was outlined with a marker at 2, 4, 7, and 11 days. The minimum and maximum diameters of each colony at each measuring time were averaged and used for the analysis. For this paper only the average colony diameter at 11 days was used in the analysis. Analysis of variance (ANOVA) was used to compare the efficacy of each chemical at 1X concentration, a Tukey-Kramer analysis was performed to compare different compounds.

Potted Saplings Experiment

A total of 80 saplings of coast live oak (*Q. agrifolia*) with calipers ranging from 3 to 6 cm, and heights between 3 and 5 m were used in the experiment. The saplings, grown in 15-gallon containers, were covered with a 50 percent shade cloth, and drip irrigated daily. On August 10, 2000, 75 saplings were inoculated on their East facing side with *P. ramorum*. One of five isolates was inoculated on each sapling in the following way. A cork borer (diameter 1.2 cm) was used to cut the bark at 1 m from the root collar; a 0.8 cm plug of agar obtained from the edge of a colony was placed in contact with the cambium, the bark plug was replaced on top agar and sealed with grafting wax. All inoculation points were wrapped in foil. On October 31, a second inoculation was performed at 10 cm from root collar, and facing North on each sapling as described above. Three days after the second inoculation, the chemical treatments, including a plain water control, were administered. Each tree was injected with 10 ml of either water, 0.1 percent copper sulfate pentahydrate, 5 percent phosetyl-Al, 11 percent metalaxyl, or 9 percent phosphorous acid. Each treatment included 15 saplings. A total of 5 saplings were mock inoculated by placing a plug of sterile agar in the wound.

On March 3, 2001, the trial was terminated. The bark around each inoculation point was carefully removed until the canker necrosis in the cambium was visible. For each inoculation 4 measurements were taken starting from the center of the inoculation plug: upwards towards the crown, downwards towards the roots, clockwise across the stem, and counterclockwise across the stem. Four isolations were performed by plating on pimaricin-ampicillin-rifampicin-Pentachloronitrobenzene (PARP) medium (Erwin and Ribeiro 1996) a chip from the further edge of the canker in each of the four directions. ANOVA was performed to compare lesion size across treatments. In this paper, we present only analyses performed on the sum of longitudinal and transversal growth values.

Results and Discussion

In Vitro Tests

Figure 1 summarizes the results of the “in vitro” tests. While several compounds resulted to be actively reducing or totally inhibiting the growth of *P. ramorum* in culture, not all compounds were equally efficacious as indicated by the variation in ED_{50} levels, and by different efficacy as indicated by ANOVA performed on data from 1X concentrations *(fig. 2)*. While some compounds like metalaxyl are effective even at minimal concentrations, others like the copper sulfate formulation used in this trial lost efficacy quite rapidly with decreasing concentration. In the case of trunk topical treatments, where chemical action is expected to occur by contact (prevention or eradication of infections), chemical concentration is a minor issue, if within the range of environmental and human safety. In the case of foliar applications, soil drenches, or injections, effective concentration is an extremely important issue. Although some chemicals may be effective against the pathogen at certain concentrations, these same chemical concentrations may be phytotoxic to the plant.

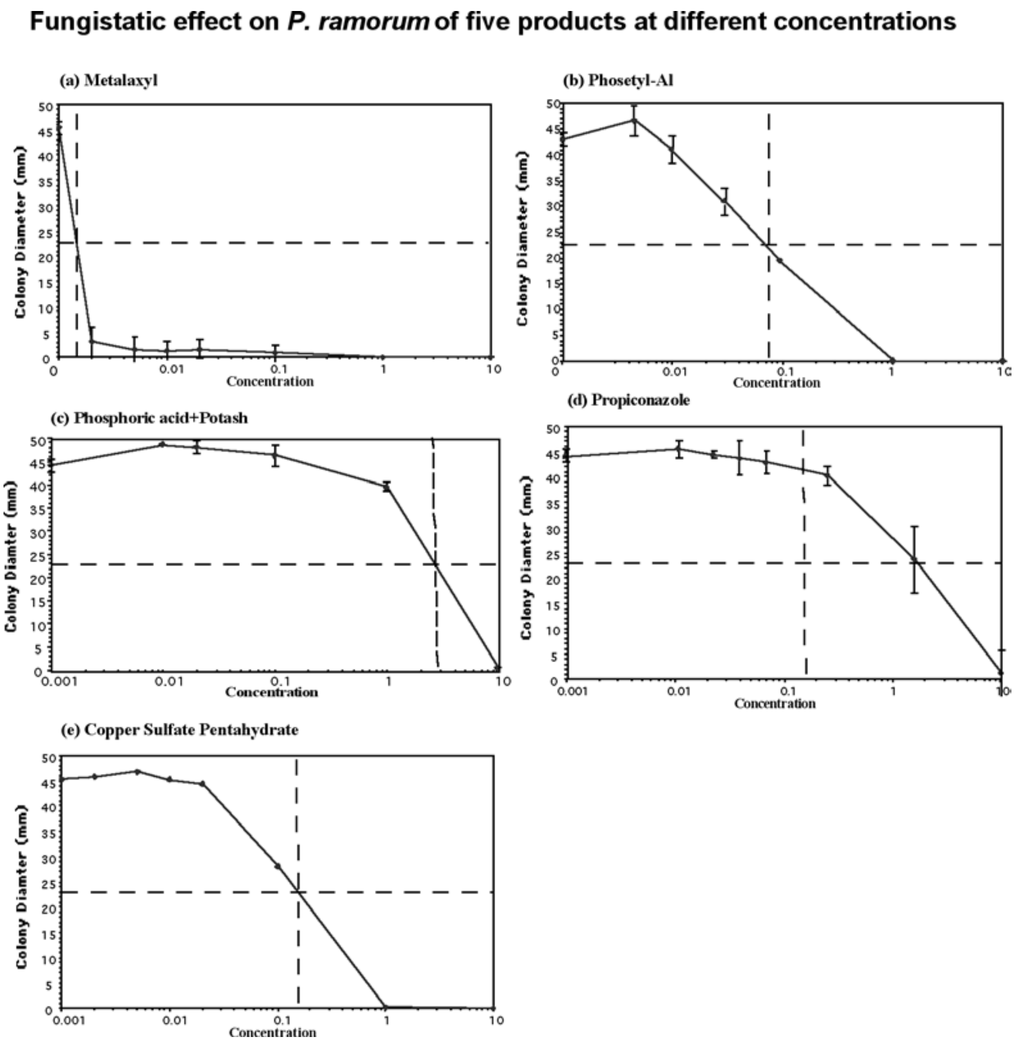

Figure 1—Mean colony diameter of *P. ramorum* 11 days after inoculating Petri dishes filled with growth medium amended with different concentrations of each chemical compound used in this trial is shown on the Y axis. Data are shown individually for each compound (panels a to e). A solid line connects the control on the Y axis (e.g., mean colony diameter of *P. ramorum* on unamended growth medium) and mean diameter values of *Phytophthora* colonies at each tested concentration. Standard deviations are shown as horizontal solid bars.The X axis is in logarithmic scale. For each compound, an approximate ED_{50} value (e.g. the concentration needed to obtain a 50 percent reduction of colony size), is indicated by the intersection of the vertical dashed line and the X axis.

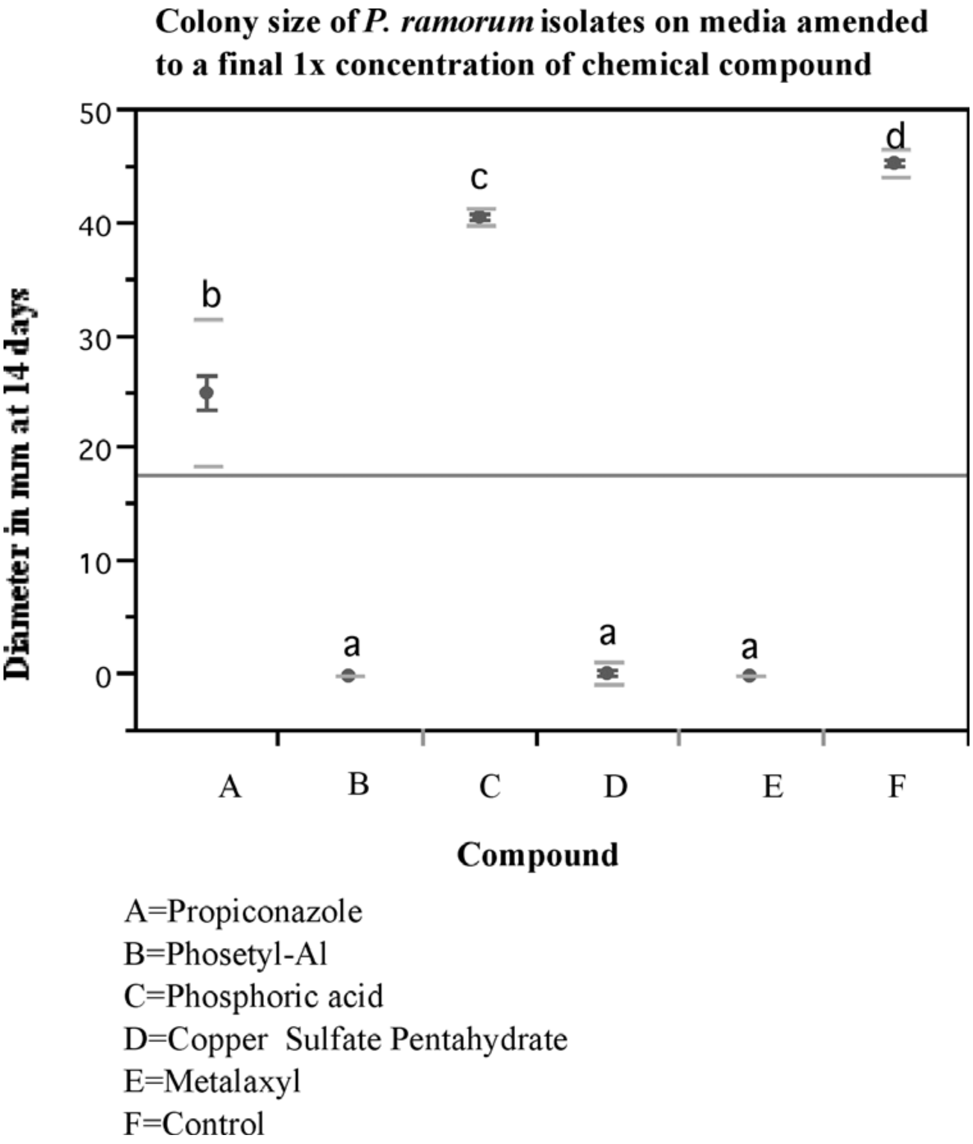

Figure 2—ANOVA results of mean colony diameter of *P. ramorum* grown on media amended with chemicals up to a 1X concentration (see *table 1* and text). Letters identify treatment grouping as indicated by a Tukey-Kramer multiple range test with alpha set at 0.05. (*P=0.0001)*.

It should be noted that some compounds, for instance phosetyl-Al, phosphites, and phosphonates are known to be a lot more effective "in planta," where the active ingredient of these chemicals, phosphorous acid, is released. For these and similar compounds, results from "in vitro" testing have limited value. It should also be noted that the mechanisms of action of each compound are different and need to be taken into account when selecting a treatment. For instance, while metalaxyl was undoubtedly the most powerful compound against *P. ramorum*, it is also known that other *Phytophthora* species can develop resistance to metalaxyl through sexual recombination. The potential for the selection of metalaxyl-resistant strains suggests a minimal use of this chemical until more is known about the biology of the pathogen.

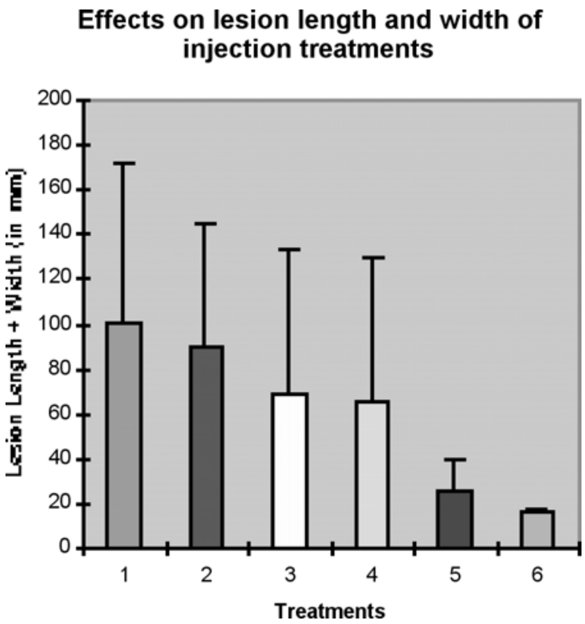

Figure 3—Lesion length+width of inoculated *P. ramorum* on *Q. agrifolia* saplings after chemical treatments. Pathogen inoculations occurred in the fall of 2000, and treatments were performed 72 hours after inoculation. 1=untreated, 2=copper sulfate (picrocubic), 3=metalaxyl, 4=phosetyl-Al, 5=phosphorous acid (phosphite), 6=mock inoculated. Both Tukey-Kramer and pairwise comparisons indicated that at alpha set at 0.05 no statistical significance was found between untreated saplings and the copper sulfate treatment. All other treatment were statistically different from the water treatment. The most effective chemical was the phosphite. Mean lesion size in saplings treated with this compound were not significantly different from lesions created by wounding only without pathogen inoculation.

Results from our "in vitro" tests provide us with several potentially valid options for chemical treatments. Copper compounds may be used for preventive coating of the trunks, phosphorous acid and metalaxyl may be used for curative treatments. Further testing in planta is required before the actual efficacy of each treatment can be evaluated.

Potted Saplings Experiment

At least three chemical compounds were effective in reducing pathogen growth rate. Saplings injected with phosetyl-Al, metalaxyl, and phosphorous acid had significantly smaller cankers than saplings untreated or injected with copper sulfate pentahydrate. Statistical significance was at the 5 percent level for cankers treated 72 hours after inoculation (DF=79, Fratio=3.97, P=0.003) *(fig. 3)*. For 10-week old cankers, identical trends were observed but statistical significance was obtained only at the 24 percent level, once the mock inoculated saplings were excluded from the analysis *(fig. 4)*. The reason for lack of strong statistical significance was clearly linked to the fact that growth rate of the pathogen inoculated in the summer slowed down significantly after a few weeks, and may have come to a complete halt. The slow-down or halting of fungal growth may not have allowed for a stronger differentiation among treatments. This interpretation is supported by the observation that in control saplings (e.g. saplings that were inoculated, but went untreated), 5-month old lesion were significantly (*P*=0.08) smaller than 2.5-month lesion (t-test=1.8, DF=28). Success of pathogen isolations from older cankers was also significantly lower (data not shown) than isolations from younger cankers. These results may indicate that either older inoculations were negatively affected by a hot spell in the early fall (temperature reached 40° C), or that saplings only allow for a maximum size of canker development, reached in this case in about 2.5 months for both inoculation trials.

Further studies need to verify whether canker size is positively correlated with disease development. Only when that correlation will be verified, the full beneficial potential of these chemical treatments may be understood. Further studies are also needed to determine potential negative collateral effects of these treatments, as well as optimal rates of active ingredients, ideal time and methods of application.

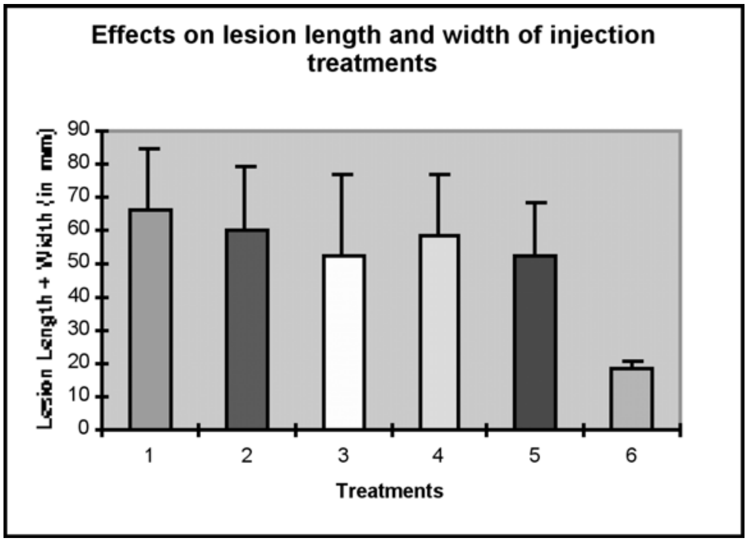

Figure 4—Lesion length+width of inoculated *P. ramorum* on *Q. agrifolia* saplings after chemical treatments. Pathogen inoculations occurred in the summer of 2000, and treatments were performed 11 weeks after inoculation. 1=untreated, 2=copper sulfate pentahydrate, 3=metalaxyl, 4=phosetyl-Al, 5=phosphorous acid (phosphite), 6=mock inoculated.

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Distribution of *Quercus agrifolia* Mycorrhizae Deep within Weathered Bedrock: A Potential Mechanism for Transport of Stored Water[1]

M. Bornyasz,[2] R. Graham,[2] and M. Allen[2]

In southwestern California, *Quercus agrifolia* distribution closely matches regions of granitic regolith. High annual evapotranspiration demand and inherent shallow soil conditions lead to a dependence on a deep rooting system and an ability to access water from deep within the regolith. Most of the plant available water in weathered granitic rock is held within micropores, which are generally too small for roots to access. It is not clear how water held in the rock matrix reaches the roots, which are confined to the fractures. Hyphae are narrow and able to explore a greater substrate volume for resources. Our study addresses the vertical composition of both endo- and ecto-mycorrhizae in weathered granitic rock in an effort to determine if mycorrhizae are available to act as conduits to transport water from rock matrix to roots. Water status, morphology, nutrients, root and mycorrhizae distribution of three *Q. agrifolia* trees were characterized from a 15-meter-wide by 4-meter-deep profile consisting of 30 to 70 cm of soil and 330 to 370 cm of weathered bedrock. Plant available water within the soil fraction was depleted by the end of June; therefore plants must rely on water available within the fractured bedrock for the remainder of the growing season and during the dry season. Roots greater than 1 mm are present throughout the entire 4-meter deep profile. Fine roots <1 mm are also present in the weathered bedrock and commonly occur in root mats consisting of live and dead roots. Percent infected tips and morphotype abundance in samples collected from the soil fraction (0-10, 10-20, 20-30 cm) decreased with depth from 65 percent to 30 percent and 12 to 2, respectively. This is a similar trend to what is generally reported in the literature. However, samples collected from fractures within the weathered bedrock at and below a one-meter depth also contained infected root tips. Percent infected tips ranged from 0-64 percent and morphotype abundance ranged from 0-10. Percent-infected tips from a 3.7 m deep rock sample closely matched that of a surface soil sample (63 percent rock; 65 percent soil), however morphotype abundance was substantially lower.

Morphotypes varied with depth and across substrates, but Cenococcum sp. was dominant in most samples that contained mycorrhizal roots and occurred throughout the entire profile. Presence or absence of mycorrhizae deep within the regolith may

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[1] This paper summarizes a poster that was presented at the Fifth Symposium on Oak Woodlands: Oaks in California's Changing Landscape, October 22-25, 2001, San Diego, California.

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be a function of substrate and not a function of depth. Live roots and infected tips were absent in samples that contained clay dominated fracture-fill material. Percent soil moisture is highest in this fracture-fill material, but the water is held tightly by the material and is less available to plants and fungi. Exploration by hyphae and persistence of mycorrhizae is also prohibited by the presence of discontinuous pore spaces created by shrink-swell behavior inherent in smectitic clays. In conclusion, mycorrhizae exist deep within the weathered granitic regolith. Nutrient acquisition may not be the primary function of this relationship. The primary function is more likely water acquisition.

Likeliness to Pay for Oak Woodlands by the Residents of San Luis Obispo County[1]

Sarah P. Cross[2]

The golden hillsides with scattered oaks, known throughout California, are decreasing each day. Some oak woodlands are being developed into residential and commercial communities while other woodlands are being converted into intensive agriculture, such as wine grape production. This continued decrease in oak woodlands has led some lawmakers to create preservation ordinances and policies to protect the remaining oaks. In areas where there are no woodlands protection policies, are residents likely to pay for the oak woodland preservation?

The purpose of this study is to determine if residents are likely to pay for oak woodland protection and to describe characteristics of the residents likely to pay.

A discrete double-bound contingent valuation survey was conducted in San Luis Obispo County during September 1997. Photos of three stages of oak woodlands development were used to illustrate for the respondents oak woodland development common throughout the county. These stages were:

State 1—Woodland areas undeveloped except for livestock production,

State 2—Areas with moderate to high intensive agriculture and ranchette style housing,

State 3—Areas with high density housing and shopping malls.

The survey was completed in two iterations with the payment values being increased in the second iteration, for a combined sample size of 300. Socio-demographic data was also gathered from the 300 respondents. Discriminant analysis was used to characterize the respondents' likeliness to pay while factor analysis was used to examine trends of the respondents.

All of the data presented in project tells a mixed story, however, it does show that there is support for oak woodland protection to some extent. The hypothesis testing has shown that San Luis Obispo County residents are likely to pay for oak woodlands. However, the payment value, stage of woodland conversion, and demographic trends differ greatly.

Future direction for the data gathered would be education to the policy makers in the region to make them aware of how the residents in San Luis Obispo County responded to this pressing issue. Determining what the willingness-to-pay for oak woodlands in San Luis Obispo County is the next step with the data collected.

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[1] This paper summarizes a poster that was presented at the Fifth Symposium on Oak Woodlands: Oaks in California's Changing Landscape, October 22-25, 2001, San Diego, California.

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Examining Effects of Vineyard Development on Bird Populations of California's Oak Woodlands—Use of GIS and Power Analysis to Select Study Sites[1]

Emily Heaton,[2] Colin Brooks,[2] Adina Merenlender,[2] Mark Reynolds,[3] and Mary Chase[4]

Vineyard expansion into California's oak woodlands is creating an increasingly fragmented and altered landscape for wildlife. This landscape-level study is designed to provide information about the effects of vineyard development and oak habitat retention on oak-associated bird communities in northern coastal California. We have used Geographic Information System (GIS) technology to identify potential study sites in Sonoma County that are hypothesized to be differentially influenced by vineyard development, or "vineyardization." Degree of vineyardization was determined using a 1997 map of vineyards and a "sliding window" GIS analysis that examined the amount and distribution of vineyard within a 2,000 m radius. Sampling sites will be established in high, medium, and low-level vineyardization areas containing low elevation (0-300 m), gently sloped (0-15 degrees) oak woodland habitat. Sites will also be established in vineyards in high-level vineyardization areas. We have also conducted an analysis of species detectability using existing bird data collected in oak woodland habitats to determine statistical power and sample sizes necessary to detect differences in certain bird populations in these habitats. Surveys of bird communities, using standard point count survey protocols, will be conducted within the various treatments over the next 3 years.

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The Status of Island Scrub Oak *(Quercus pacifica)* on Catalina Island, California[1]

Denise A. Knapp[2]

The island scrub oak is characterized by a shrubby (to 2 meters) or arborescent (to 5 meters or taller) growth form. It is the dominant species of the scrub oak chaparral community on Catalina Island, which occupies approximately 25 percent of the 76 square-mile island, primarily on north-facing slopes. The Santa Catalina Island Conservancy, which owns and manages 88 percent of the island, is actively working to protect, monitor, and restore this unique plant community. This includes investigating the cause of a large-scale oak dieback, monitoring health, growth, and reproduction, reducing feral animal impacts, and propagating young oaks for restoration.

A large-scale die-off threatens the health of the scrub oak community on Catalina Island. This pattern was noted by Conservancy personnel as early as 1995. It is patchy in distribution, and appears to be concentrated on the Channel side of the island. Island residents have noted episodic oak mortality in the past; this appears to be cyclical in nature, possibly coinciding with moisture patterns.

An oak root rot fungus in the genus *Armillaria* was found in both the northeast and northwest areas of the island. This is a naturally occurring fungus that usually takes a long time to affect the tree. These trees have most likely been infected for decades. Investigations have revealed no sign of the Oak Mortality Syndrome fungus, *Phytopthora*.

The less pathogenic species of *Armillaria* tend to invade when the trees are stressed by environmental factors. The prevalence of dying trees on the Channel side of the island suggests air pollution as a potential stressor. Future research is needed to investigate the distribution of trees which are dying from this fungus and several different environmental factors such as water potential, slope/aspect, and air pollution. Also illuminating would be a demographic study of the island's scrub oak populations through either dendrochronology or Carbon dating.

The presence of non-native animals on the island has greatly inhibited regeneration of the island scrub oak. Feral pigs, mule deer, feral goats, and American bison have variously reduced regenerative potential and damaged scrub oak habitat. Feral animal removal efforts in the last decade by the Conservancy's Ecological Restoration Department have concentrated on goats and pigs, and are nearing completion.

In order to maintain or enhance the natural structure of Catalina Island's plant communities, a pilot monitoring study was initiated in 2001. The objectives of this

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study are: 1) to provide detailed descriptions of the variability of stand structure, health, and regeneration of island scrub oak trees (*Quercus pacifica*) to use as a general model for restoration and maintenance management, and 2) to investigate the influence of herbivory on the dynamics of this species.

Two locations predominantly supporting scrub oak habitat were selected for the study: the west end and airport areas of the island. The west end has had all feral animals except deer removed since the mid- to late-1990s, thus providing an impact comparison. Four permanent plots have been located randomly within each area, and more will be added in the future.

Plots are 30 meters by 6 meters. The plot is divided into five 6 by 6-meter subplots within which each individual rooted within the plot is mapped. For each individual, the following parameters were recorded: number of stems/trunks, basal diameter of the largest three trunks, age class, overall health, animal/pest damage, and acorn production. In addition, the following is recorded for seedlings and saplings: substrate (litter or bare ground), whether or not is immediately associated with annual grasses, and whether or not is growing under the cover of another species.

The number of mature trees per plot ranged from 3 to 13. Dead trees comprised an average of 26 percent of the trees in each plot, and was 100 percent in one plot. Saplings were found in only two of the eight plots studied, with one and four saplings found (25 percent and 14 percent of all individuals, respectively). Seedlings were found in 3 of the 8 plots studied, with one seedling found in each of two plots and 21 seedlings found in one plot. The majority of trees had an acorn production class of 0 (no acorns), 1 (a few seen after close scrutiny), and 2 (a fair number, acorns seen readily).

Island scrub oak outplanting trials were begun in 1999 in preparation for future large-scale restoration efforts. The trials involve the planting of oak seedlings and acorns with several different soil, watering, and depth treatments. James H. Ackerman Native Plant Nursery staff, with the help of many volunteer hours, have been actively collecting acorns from island scrub oak trees and raising them to saplings for this project.

Multi-scale Data to Assess and Monitor Sudden Oak Death[1]

Lisa M. Levien,[2] Chris S. Fischer,[2] Lianne C. Mahon,[2] and Jeff A. Mai[2]

The USDA Forest Service (FS) and California Department of Forestry and Fire Protection (CDF) are monitoring Sudden Oak Death (SOD) under the umbrella of the larger California Land Cover Mapping and Monitoring Program (LCMMP). The LCMMP is a statewide cooperative effort among the FS and CDF focused on mapping and monitoring California's vegetation and land cover.

Under the LCMMP the FS and CDF conduct change detection as a basis for monitoring and for identifying land cover change across all ownerships. This program has successfully used satellite imagery and change detection techniques to map and monitor changes in vegetation due to drought-induced insect mortality, fire mortality and subtle changes due to selective harvest methods. The current project has been easily adapted under the larger program to identify oak mortality, potential SOD areas and develop a basis for establishing a monitoring program for SOD.

The distribution of SOD in California might stretch from the Oregon border to Monterey County, however, to date there are 10 counties confirmed with SOD. These 10 counties are included in the project area that spans Humboldt County in the north to Monterey County in the south.

The objective of the SOD project is to use multi-scale remotely sensed data to identify "hot spots" of oak mortality, and verify these areas with a combination of airborne imagery, aerial surveys and field verification. Given the size of the affected land area, detection and monitoring SOD would not be practical without the use of remotely sensed data.

Landsat Thematic Mapper (TM) satellite imagery was acquired for two time periods, July 1994 and May 2000, to detect changes in oaks and develop a base from which to identify and map oak mortality. Land cover changes are derived from the TM imagery, employing a multi-temporal Kauth–Thomas transformation. This process produces three components, a greenness component, brightness component and wetness component. These components portray subtle differences in land cover. If a group of trees experienced mortality during the 1994 and 2000 timeframe it would be indicated in the levels of greenness, brightness and wetness, possibly less wet and green, and more bright. Vegetation data is used to stratify the brightness,

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greenness, wetness image into lifeform and change. Unsupervised image classification is performed and each resultant class is placed into a particular change class, according to its level of change.

Areas depicting large decreases in change were evaluated with existing fire history and stand history data. Areas of small decrease were further evaluated to determine the potential for change due to oak mortality. Vegetation layers, spectral reflectance values, comparison to aerial imagery from known SOD affected areas, and other ancillary data were used to assist in this labeling process. If mortality due to SOD was suspected, the class was then labeled as potential SOD. Because of the possibility that areas of potential SOD might be eliminated during an aggregation process this particular class has been left at the pixel level. Additional remotely sensed data of various scales including two-meter digital camera imagery were acquired from flights over affected counties and adjacent areas. Digital camera data in conjunction with the satellite imagery were analyzed to identify the extent of oak mortality. Each photo was examined for signs of hardwood mortality that could not be attributed to known cause. Areas of potential SOD were compared to the digital camera data for further confirmation of mortality. In areas of confirmed SOD the digital camera data provided a valuable reference tool and allowed for a more detailed assessment of both the visual appearance of SOD, as well as the extent of the mortality. As a final step in the validation process an accuracy assessment will be performed.

Aerial surveys provide another means for detection, monitoring and calibration, and discrimination of various spectral reflectance values important to image classification. The surveys were conducted from a fixed-wing aircraft over a period of three days using a crew of two and a pilot. Approximately 10 million acres of California's coastal hardwood rangelands and mixed hardwoods were surveyed. Mortality areas were identified visually, sketch mapped, and photographed on 35mm color film. A handheld global position system (GPS) was used on the aircraft to record the flight line and pinpoint potential SOD sites. The GPS line and point data were exported to aid in creating a geographic information system (GIS) coverage of mortality areas. The combination of GPS, photography, and detailed notes were used to map and characterize potential areas of mortality. Field verification is currently being performed to confirm or refute presence of the disease and evaluate the accuracy of the survey and change data.

This collaborative effort is essential to a low-cost, long-term monitoring and sampling strategy for SOD. These data are prerequisite for identifying future management opportunities that include allowing for more focused field efforts, acquiring future data more efficiently and providing a critical look at current SOD related mortality conditions. The resultant maps will provide a baseline for future monitoring efforts and may streamline field confirmation of areas affected by SOD.

North Coast Oak Woodland Conservation Research on a Landscape Scale[1]

Adina Merenlender,[2] Colin Brooks,[2] Jodi Hilty,[3] Emily Heaton,[2] Kerry Heise,[2] and Jeff Opperman[2]

A diverse suite of projects will be depicted demonstrating the value of mapping, monitoring, and modeling the North Coast's changing oak woodland landscape. This applied research uses a geographic information system to better integrate biodiversity research and conservation planning in California's north coast oak woodlands.

This work is designed to map natural resources and forecast land use change in order to identify natural resources at risk. The primary threats that oak woodlands face in the north coast are: 1) population growth resulting in urban and sub-urban expansion, 2) a booming wine industry driving an expansion of hillside vineyards in oak woodlands, and 3) the cascading effects of land-use on the Russian River Basin. We have GIS analysis that allows examination of these processes and have developed a vineyard and residential expansion model for Sonoma County.

To assess the effects of land-use conversion on biodiversity, we have measured biological community integrity and diversity in various land use types and oak woodland habitats. These include suburban developments, small ranches, vineyards, riparian areas, and undeveloped woodlands.

County planners and others are using the products that have resulted from this research to gain an understanding of regional level changes and conservation priorities.

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[1] This paper summarizes a poster that was presented at the Fifth Symposium on Oak Woodlands: Oaks in California's Changing Landscape, October 22-25, 2001, San Diego, California.

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Utilization Implications for Hardwoods Susceptible to Sudden Oak Death[1]

John R. Shelly[2]

The number of woody species succumbing to Sudden Oak Death (SOD) infections and the number of counties where the pathogen has been reported continue to increase. One result is that the hazards related to falling trees and high levels of fuel hazard conditions are also increasing dramatically. The removal of infected, dead and dying trees creates numerous handling and disposal problems. One possible solution is to develop markets for wood products made from SOD infected material that would help defer some of the cost of removing the hazards and reduce the amount going into landfill. The results of a recent project that focused on tanoak (*Lithocarpus densiflorus*) utilization, one of the SOD susceptible species, provide valuable insight into the potential for utilizing SOD infected material.

Tanoak was found to have very good woodworking properties that make it a viable resource for furniture, flooring, and other value-added products. However, because of some unexpected inherent physical and chemical properties, about 80 percent of the lumber value was lost to defects that were introduced into the lumber when it was kiln dried. Cell collapse was responsible for about 1/3 of this loss and the remainder was due to enzymatic stain. Special manufacturing techniques and drying schedules are needed to minimize these defects. Results indicate that tanoak logs need to be processed into lumber soon after the trees are harvested and that fresh cut lumber must immediately begin drying in a moderate temperature/low humidity environment. Delay in drying will result in unacceptable stain. However, initial drying at temperatures above 100 degrees Fahrenheit dramatically increase the potential for other drying defects. A recommended drying schedule is reported. These difficulties encountered in processing tanoak emphasize the need to fully understand the properties of any SOD infected material being considered for value-added processing.

For utilization of SOD infected material to be a realistic option it is necessary to develop an understanding of the amount of material that could be available for utilization, the quality of the infected wood, and what types of products are feasible. A series of utilization studies were recently initiated at the UC Forest Products Laboratory focused on inventorying SOD infected wood in Marin County and determining the physical and chemical properties of representative samples of infected wood at various stages of SOD disease. The objectives of this study are to determine the relationship between pathogen initiation and the rate of wood

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deterioration; and to define protocols, guidelines, and recommended utilization practices for the inventory, removal, transport and manufacturing of value-added products from SOD infected material. The specific project objectives include:

- Analyze the rate of wood deterioration in SOD-infected material,
- Determine risk of using infected wood in existing disposal/utilization enterprises,
- Develop recommendations for handling, transporting and processing infected material,
- Analyze the technical feasibility of using SOD-infected material for wood products including particle and fiber composites, solidwood, and fuel and firewood (chips, firewood, and densified fuel), and pulp,
- Assess the risk of pathogen survival in processed products.

Preliminary results suggest that the primary pathogen, *Phytophthora* has little or no direct effect on wood quality but that the secondary pathogens (hypoxylon and ambrosia/bark beetles) have the potential to seriously and rapidly deteriorate wood quality. If trees with low natural resistance to insect and decay attack are not removed before the final stages of SOD disease it is unlikely they can be used for any value-added products except landscape materials (mulch/compost) or soil amendments. Although this observation suggests the early removal of infected trees, the advocacy of such a policy would compromise the species ability to develop natural resistance to the *Phytophthora* pathogen. This and other utilization questions need additional research. Trees with natural resistance would likely have more utilization potential and this will be explored in the final stages of the current project.

Value of Oak Woodlands and Open Space on Private Property Values in Southern California[1]

Richard B. Standiford[2] and Thomas Scott[3]

Rapid urbanization of California's oak woodlands is having a pronounced effect on its ecological values. These areas are sought out for new residential sites to a large degree because of their amenity values. In response to this rapid exurban migration, there has been an increase in use of conservation easements and purchase of development rights by land trusts and other entities to maintain large blocks of open space. However, the effect of dedicated open space on land markets is not known. This project is designed to quantify how aesthetic and environmental values of adjacent oak woodland open space is captured in parcel sale prices. These economic factors affect property tax revenues for a particular area, as well as having a potential for new mechanisms to fund open space purchases for conservation purposes. This pilot study was carried out in the Santa Rosa Plateau area of Riverside County, the site of an 8,300-acre reserve owned and managed by The Nature Conservancy (TNC). It is surrounded by one of the most rapidly growing urban areas in the state.

Information collected on the 4,800 parcels immediately surrounding the open space reserve included: property size and location; property improvements (house size, number of bedrooms, pools, out-buildings, fences, etc.); amount and date of the most recent sales transaction; current assessed value of the land and structures; and current zoning. Distance from each parcel to the edge of the open space land, to the nearest trailhead and to the nearest native oak stand was calculated using a geographic information system. Hedonic regression was used to develop a multivariate model of land and home value. Both land and home value decreased as distance from the open space boundary and local stands of native oak habitat increased. The model results were applied to all individual parcels in the study area, and summed up to evaluate open space values on the entire community. A 10 percent decrease in the distance to the nearest oak stands and to the edge of the permanent open space land resulted in an increase of over $20 million in the total land and home value.

This study shows how hedonic prices can be used to evaluate the relative value of open space on individual house and land prices, as well as on an overall community's value. It is clear that natural resources in a broad geographic area contribute to the economic value of real property. This increased value provides an

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economic incentive for investing in conservation. These results will be used in the future to model different open space conservation and oak restoration strategies. Optimal economic patterns of open space design and restoration will be compared to conservation biology principles of optimal reserve design. The increasing scarcity of natural resources in rapidly urbanizing areas is resulting in economic values that are reflected in both individual and community economic values. This study shows promising results that can be used to evaluate how public and private investments in conservation and restoration can be justified in economic terms.

Oak Restoration Trials: Santa Catalina Island[1]

Lisa Stratton[2]

Two restoration trials involving four oak species have been implemented as part of a larger restoration program for Catalina Island. In 1997 the Catalina Island Conservancy began an active program of restoration after 50 years of ranching and farming activities on the island. The restoration program includes removing feral goats and pigs island-wide and converting 80 acres of old hayfields in Middle Canyon to native plant communities. This conversion presented the opportunity to implement experimental restoration trials to test the efficiency and efficacy of a variety of restoration techniques. The primary challenges to restoration in these areas include bison disturbance, deer browsing, long dry seasons and disturbed, weed saturated soils (e.g., *Avena fatua, Cynodon dactylon* (Bermuda grass), *Phalaris aquatica* (Harding grass) and incipient populations of *Foeniculum vulgare* (fennel) and *Nicotiana glauca* (tree tobacco).

In 1999, an island scrub oak seedling trial (*Quercus pacifica*) was initiated to compare three different watering treatments: 1) a commercial time-release product, Driwater, 2) monthly deep-pipe watering and, 3) unwatered controls. This trial is also a factorial design that includes a native soil component. Soil from beneath mature oaks, potentially containing spore from the oak ectomycorrhizal associate, was added to half the holes at planting time. After two years the seedlings receiving the monthly watering supplements in the deep pipes were significantly taller ($p<0.001$) than either the no water or Driwater product treatments (45 inches vs. 33 and 29 respectively). Survivorship was higher for the deep pipe treatment (98 percent vs. 94 percent for the other two), but not significantly different.

After 2 years, in December 2000, all watering supplements were discontinued to evaluate their relative effectiveness in preparing the seedlings for long term survival. While the deep pipe treatment continued to outperform the other treatments in terms of survivorship (96 percent vs. 92 percent for other treatments) and growth, overall survival for all treatments was high and differences in height were only significant between the deep pipe (60 in) and the driwater treatment (46 in) ($p<0.001$). Seedlings with native soil added have increasingly higher survivorship each year (from 1999 [99 percent vs. 97 percent] to 2001 [96 percent vs. 90 percent]). Seedling height between soil treatments, however, does not differ at all. While measurements of carbon assimilation in 2000 indicate that seedlings with native soil had significantly higher photosynthetic rates than those without (4.1 vs. 2.65 umole m^{-2} s^{-1} CO_2), those

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differences disappeared in 2001 after watering treatments had been discontinued for 9 months.

Based on the success of the unwatered seedlings in the 1999 trial (96 percent survival), an unwatered trial using acorns was initiated in 2001. This acorn trial is a factorial experiment which compares four factors: 1) site (within and adjacent to a drainage), 2) augered (refilled) and un-augered planting sites, 3) with and without leaf litter and 4) species (four species: *Quercus pacifica, Q. tomentella, Q. chrysolepis, Q. x macdonaldii*). Twelve-hundred acorns were planted 3 per hole in 400 planting sites in proportions reflecting their frequency on the island. *Quercus pacifica* (island scrub oak; n=768) is the most common species and dominates most of the oak woodlands on the island. *Quercus tomentella* (island oak; n=144), *Q. chrysolepis* (canyon live oak; n=144) and *Q. x macdonaldii* (Macdonald's oak; n=144) are less frequent. Weed competition is inhibited with 1-m^2 weed mats. All seedlings are protected with tree-tubes (Tree Essentials, Inc.)[3] against deer; however, bison regularly scratch themselves on the stakes supporting the tree-tubes and knock them over. Overturned tubes expose saplings to overheating, breakage, and potential deer herbivory.

Results from an initial spring monitoring indicate that significantly ($p<.009$) more acorns covered in oak leaf-duff germinated than those without (153 vs. 101). In terms of species, the highest overall rate of germination was 38 percent (*Q. tomentella*). Because three acorns were planted per planting site, a 'site-rate' for germination is tallied. For example, if 48 of 144 overall germinate then the germination rate is 33 percent, but if they occur in all 48 planting sites then the site rate would be 100 percent since all planting sites had seedlings. *Quercus tomentella* also had the highest site-rate (69 percent). *Quercus chrysolepis* had an overall germination rate of 27 percent and a site-rate of 56 percent. *Quercus x macdonaldii* had an overall germination rate of 18 percent and a site-rate of 36 percent. *Quercus pacifica* had the lowest overall germination rate (17 percent) and a low site germination rate (39 percent). We expect the other factors—e.g., proximity to a drainage and pre-augered holes—to show their effects when the roots get deeper. Survivorship over the summer followed patterns similar to the initial germination rates for species and mulch treatments. Seedlings grew an average of 3 to 6 inches and differences in height were not significant between treatments.

The primary lessons from these trials are that oaks can survive without added water when outplanted as either acorns or seedlings, that leaf mulch facilitates acorn germination and that placing multiple acorns in a planting site will enhance the chance of getting a seedling in a particular site. Establishing oak trees that stand firmly above the browse line is the first step in restoring an oak community to Middle Canyon.

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[3] Mention of trade names or products is for information only and does not imply endorsement by the U.S. Department of Agriculture.

Rehabilitation of an Oak Planting Project on Cleared Rangeland Using Treeshelters and Grazing: A Ten-year Saga[1]

Jerry Tecklin,[2] J. Michael Connor,[2] and Douglas D. McCreary[2]

On a 2-hectare site at the Sierra Foothill Research and Extension Center near Marysville, California, 1,440 blue oaks (*Quercus douglasii*) were planted during 1990-91 in an attempt to re-vegetate an oak woodland that had been almost totally cleared for cattle grazing during the mid-1960s. This initial planting of acorns, 4-month old seedlings, and 1-year-old bare-root plants was aggressively depleted by mainly grasshoppers (*Melanoplus devastator*) and rodents (*Microtus californicus*). After 2 years we replanted areas that had experienced total mortality with treeshelter-protected acorns and seedlings. In another remediation effort we selected pairs of stunted survivor seedlings (average height 16 cm) and retrofitted one of each pair with a treeshelter to test if this would be an effective way to increase height growth and survival. In 1997 we divided our planted area into two parts separated by electric fence and grazed one part, leaving the other part ungrazed. This was an attempt to discourage rodent predation which continued to be exacerbated by dense annual grass cover resulting from the exclusion of grazing, which had been our practice when the project was initiated. Using cattle to reduce rodent cover also provided an opportunity to test the effect of grazing on our re-vegetation effort. Our remediations employing treeshelters have resulted in sapling-sized trees (average height of ungrazed vs. grazed = 2.1 vs. 1.9 m), while those unprotected remain in stunted condition (average height of ungrazed vs. grazed = 0.5 vs. 0.3 m). Cattle grazing for short periods in winter and spring has done only minor damage to treeshelters, minor to moderate damage to the oaks after each grazing exposure, and reduced rodent cover and rodent damage dramatically. There is now almost no rodent damage to oaks in the grazed area, but this benefit of grazing has been offset by lesser growth of our grazed trees. The cumulative impact of several years of minor browsing of trees in the grazed area has reduced their crown volume, as compared to the apparent larger crowns of our ungrazed trees, and probably results in the significantly smaller height and girth observed in our grazed trees.

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[1] This paper summarizes a poster that was presented at the Fifth Symposium on Oak Woodlands: Oaks in California's Changing Landscape, October 22-25, 2001, San Diego, California.

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Forty Years of Land Use and Land Ownership Change in Central Sierra Nevada Oak Woodlands[1]

Matt Wacker,[2] David Saah,[2] and Louise Fortmann[3]

The vast majority of California's oak woodlands are privately owned, and, therefore, highly susceptible to changes in land use and ownership as well as land fragmentation. This is particularly true in the Central Sierra Nevada, where significant changes in land use have occurred during the past 40 years. Perhaps no location illustrates this trend better than the Central Sierra Nevada, an area that has experienced a dramatic shift in land use away from traditional rural land uses such as timber harvesting, livestock grazing, and irrigated agriculture toward rural residential developments driven largely by an influx of new residents that began migrating into this area in the early 1970s.

Changes in land use, land ownership, and parcel size have important consequences for both cultural and natural landscapes within this region. For example, increases in rural residential settlements create management problems for nearby farmers and ranchers and drive up land prices, often leading to further land conversion. Exurban migrants may also have a different perception of how land is to be used and managed and often value rangeland and forests for their amenity values rather than for their productive capacity. These changes in socio-political values can influence local land use planning and lead to conflicts between newcomers and long-time residents. Aside from changes in land use, changes in land ownership, owner residence, and parcel size can also have important consequences for rural landscapes. Previous studies have tended to show that improved land management is primarily associated with larger parcel sizes and connectedness (in terms of both residential connections and economic connections) to the land. Thus, changes in land use and land ownership leading to decreases in parcel sizes, increases in absentee ownership, or increases in corporate ownership (to the extent that these owners are not economically tied to the land) can lead to deleterious resource management.

To analyze these changes, we used a GIS-based approach by comparing digitized versions of land holding maps from the 1950s with current digital versions of county assessor's parcel databases for two fast-growing counties in the Central

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[1] This paper summarizes a poster that was presented at the Fifth Symposium on Oak Woodlands: Oaks in California's Changing Landscape, October 22-25, 2001, San Diego, California.

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Sierra, Placer and El Dorado. Unfortunately, our choice of study area was constrained somewhat by the availability of historic land use and land ownership datasets which limited our ability to include many areas of the greatest amount of land use change in these counties. For Placer County, the study area extended from Highway 49 on the west to the crest of the Sierra Nevada on the east; in El Dorado County, the study area extended from 121 degrees west longitude (approximately a north-south line running just west of Latrobe) to the western edge of the El Dorado National Forest at approximately 120.5 degrees west longitude. Because of these differences, the Placer study area contained significantly less oak-dominated rangeland than the El Dorado study area and more Federally owned coniferous forest.

For our historic dataset, we used data originally collected by UC Berkeley researcher Dennis Teeguarden to analyze private forest ownership attributes in 1957. This data was collected by running north-south transects through the study area at approximately two-mile intervals in privately owned lands and three-mile intervals in Federally owned lands. Parcel intersection points were recorded along each transect and a set of owner attributes, including owner occupation, owner residence, and owner name were recorded for each sampled parcel. These transect and parcel sample point maps were digitized and incorporated into a Geographic Information System. Current landowner attributes were collected from digital versions of county assessor's parcel maps and intersected with the digitized Teeguarden sample transects to obtain a second GIS coverage. Through this procedure we were able to obtain two arc-based GIS datasets, one for 1957 and one for the present day, where the nodes of each arc represented the top and bottom intersection points of a parcel polygon. Using these datasets, arc length and arc count comparisons were made among different classes of land use, landowner residence, and type of landowner to assess the extent of land use and land ownership change as well as the extent of parcel fragmentation in the study areas.

Results indicate a large decrease in the amount of land devoted to agriculture and forestry in both counties. In Placer County, land devoted to agriculture, which included both grazing land and farmland, declined from 3.5 percent to 0.25 percent while in El Dorado County farmland declined slightly from 5.6 percent to 5.2 percent but grazing land dropped sharply from 41.5 percent to 5.8 percent of the study area. Land devoted to forestry decreased from 28.3 percent to 18.4 percent in Placer and from 11.4 percent to 8.7 percent in El Dorado. These decreases in rural land uses were coupled with an increase in land devoted to other, primarily residential land uses. In Placer County, these lands increased from 68.1 percent to 81.1 percent; the increase was even more pronounced in El Dorado where other land uses increased from 41.5 percent to 81.2 percent. In terms of land ownership, the most notable trends were an increase in Federal ownership and a drop in "other" (non-business) ownership within Placer County. El Dorado County also saw a drop in "other" ownerships, but, as opposed to Placer County, owners classified as businesses increased sharply. Owner residence was largely unchanged in El Dorado County while absentee ownership declined and Federal ownership increased in Placer County. Parcel size changes were characterized by marked fragmentation of land holdings across all land uses, ownerships, and owner residences in both counties.

Given these results, it appears that grazing lands in the western portion of El Dorado County have experienced the greatest amount of parcel fragmentation and land use conversion. Equally significant has been the increase of business ownership of rangelands in western El Dorado County, primarily by land developers and speculators who likely intend to convert these lands to residential uses in the future. The study area within Placer County has become increasingly characterized by Federally owned or locally owned, “other” lands (residential/recreational), both situations that would tend to retard future land use change. Additional studies are currently underway to determine how past changes in land use and land ownership have affected vegetation composition and transitions between various vegetation states at the landscape scale from the 1950s to the current day. By better understanding the relationship between land use and vegetation change, we hope to inform planners charged with regulating land use in Sierra Nevada oak woodlands of the likely consequences of poorly-planned rural residential growth and future land use change in the region.

The Oak Woodland Bird Conservation Plan: A Strategy for Protecting and Managing Oak Woodland Habitats and Associated Birds in California [1]

Steve Zack,[2] Mary K. Chase,[3] and Geoffrey R. Geupel[3]

Over 330 species of birds, mammals, reptiles, and amphibians depend on oak woodlands in California at some stage in their life cycle. California oak woodlands may rank among the top three habitat types in North America for bird richness. Oak woodlands are able to sustain such abundant wildlife primarily because they produce acorns, a high quality and frequently copious food supply. Oaks also provide important shelter in the form of cavities for nesting. Moreover, oak woodlands are among the most highly prized of California's landscapes, for both aesthetic reasons and utilitarian needs such as firewood collection and grazing.

California's oak woodlands are threatened in many ways. Ongoing loss to development and agriculture, the lack of regeneration of several key tree species, and the recent "Sudden Oak Death Syndrome" crisis are the main threats to oak woodland habitat. Today only two-thirds of California's original oak woodlands remain (approximately 7 million acres). Of those, only about 4 percent enjoy protected status. Lack of recruitment of young oaks combined with the SODS epidemic affect 7 of the 10 acorn-bearing species of oak tree in California. The combined effect of these two problems on native wildlife populations is inestimable.

The Oak Woodland Bird Conservation Plan (BCP) has been developed by California Partners in Flight to guide conservation policy and action on behalf of oak woodland habitats and wildlife, with the goal of supporting the long-term viability and recovery of both native bird populations and other native species. This BCP will serve as a repository for information, published and unpublished, on the ecology, distribution, and status of focal bird species, historic and current threats, landscape patterns, and conservation measures. This plan, along with the associated Geographic Information System (GIS) database of oak woodland habitats and monitoring data maintained at the Point Reyes Bird Observatory (PRBO), is the first iteration of a continuous process of updating habitat conservation recommendations based on the latest scientific monitoring and research data.

Designing conservation efforts for oak woodland habitats based on the needs of birds is useful because birds occupy a diverse range of niches within oak woodlands:

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[1] This paper summarizes a poster that was presented at the Fifth Symposium on Oak Woodlands: Oaks in California's Changing Landscape, October 22-25, 2001, San Diego, California.

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from those that nest on the ground to those that nest in the cavities of mature trees, those that feed primarily on insects and those that rely heavily on the acorn mast from year to year. Evidence and experience indicate that by managing for a diversity of birds, diverse oak woodland habitat structure will be maintained, and many other elements of terrestrial biodiversity will be conserved.

This BCP addresses the problems facing landbirds in oak woodland habitats throughout California and provides science-based recommendations to both public and private landowners. It outlines specific conservation action items, including detailed management, acquisition, and research recommendations, designed to heighten our understanding of how the threats and issues surrounding California's oak woodlands are and will affect the birds that are intimately connected to them.

At over 120 sites throughout California, monitoring data on oak woodland birds have been collected continuously over the past 10 years. This BCP places an emphasis on a suite of 7 bird species chosen because of their conservation interest to serve as focal species representative of the range of oak habitats in the state. Visit the Web site "http://www.prbo.org/CPIF/Oaks/oak_directory.html" to view maps of oak woodland habitat coverage, focal species ranges and PIF monitoring sites in California. Preliminary analyses of the seven focal species' habitat requirements reveal the following:

Four of seven focal species have experienced significant population declines, local extirpations, or both. The only species that appears to be significantly and consistently increasing is the western scrub-jay, a bird that adjusts readily to urbanization but is also an important nest predator of many other native bird species.

Loss of habitat or habitat structure (such as dead standing trees, mature trees with cavities, or a shrubby understory component) is implicated as a likely cause of decline and/or other problems for five of the seven focal species.

Accordingly, a series of conservation recommendations are provided, focusing primarily on protection, restoration and management of habitat that will facilitate and promote natural oak woodland regeneration. Other recommendations focus on the need to promote nest success, by retaining mature oaks in altered landscapes to provide nest cavities and by keeping down the number of native and introduced nest predators. Species-specific conservation recommendations for the western bluebird, Blue-gray Gnatcatcher and Acorn Woodpecker are also defined.

High priority conservation areas or "portfolio sites," distinguished by their protected status and potential for managing oak woodland habitat through restoration, are identified within the 10 bioregions of California as defined by the California Biodiversity Council. Through a process of adaptive conservation planning, conservation action items will continuously be derived from a synthesis of proven practices, species' distributions and ecologies, and land-use patterns. Information gaps revealed will guide future research and monitoring. The plan itself is available at the Web site: http://www.prbo.org/CPIF/Consplan.html.