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Technical Editors

Adina Merenlender is a natural resource specialist, University of California, Berkeley, Department of Environmental Science, Policy and Management, Hopland Research & Extension Center, 4070 University Road. Hopland, CA 95449. e-mail: adina@nature.berkeley.edu.

Douglas McCreary is a natural resources specialist, University of California, Berkeley, Department of Environmental Science, Policy and Management, 8279 Scott Forbes Road, Browns Valley, CA 95918. e-mail: ddmccreary@ucdavis.edu.

Kathryn L. Purcell is a research wildlife biologist, U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, 2081 E. Sierra Avenue, Fresno, CA 93710. e-mail: kpurcell@fs.fed.us.

Proceedings of the Sixth Symposium on Oak Woodlands: Today's Challenges, Tomorrow's Opportunities

October 9-12, 2006 Rohnert Park, California

Adina Merenlender, Douglas McCreary, Kathryn L. Purcell
Technical Editors

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Abstract

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The Sixth Oak Symposium provided a forum for current research and outstanding case studies on oak woodland science and sustainability in California. This symposium was the latest in a series of conferences on this subject held every 5 years since 1979. The proceedings from this conference series represent the most comprehensive source of scientific and management information on a wide range of subjects including oak ecology, hardwood rangeland management, oak restoration and conservation, woodland land-use change and planning. The conference was attended by academics, planners, conservation practitioners, foresters, arborists, and people just interested in oaks and oak-woodland conservation. Together we form a community of researchers and practitioners working toward maintaining and restoring California's oak woodlands. The findings reported here recognize: (1) the rich history and current interest that Native American communities have for oaks, (2) the inherent complexity of wildlife relationships with woodland resources, (3) the need for greater understanding of belowground processes, and (4) that the land conservation tools and policies evolving rapidly to protect and restore oak woodlands need to be evaluated. Although progress has been made, continued emphasis on research and extension is required to further California oak conservation.

Keywords: Adaptive management, conservation policy, hardwood rangelands, regeneration, restoration, wildlife ecology.

Acknowledgments

Program Committee

Adina Merenlender, UCB, CNR, ESPM, (707) 774-1270, e-mail: adina@nature.berkeley.edu
Douglas McCreary, UCB, CNR, ESPM, (530) 639-8807, e-mail: mccreary@nature.berkeley.edu
Kathryn Purcell, USDA FS, PSW, (559) 323-3200, e-mail: kpurcell@fs.fed.us
Greg Guisti, UC Cooperative Extension, (707) 463-4495, e-mail: gagiusti@ucdavis.edu
Sherry Cooper, UC Center for Forestry, (530) 224-4902, e-mail: slcooper@nature.berkeley.edu

Program Coordination

University of California Integrated Hardwood Range Management Program
University of California Division of Agriculture and Natural Resources
University of California at Berkeley College of Natural Resources

Steering Committee

Steve Barnhart, Santa Rosa Junior College
Jill Butler, California Department of Forestry and Fire Protection
Sherry Cooper, UC Center for Forestry
Lisa Fischer, USDA Forest Service, State and Private Forestry
Greg Giusti, UC Cooperative Extension and Integrated Hardwood Management Program
Bruce Hagen, California Department of Forestry and Fire Protection
Douglas McCreary, UC Berkeley, Integrated Hardwood Management Program
Adina Merenlender, UC Berkeley, Integrated Hardwood Management Program
Jake Newell, Sonoma County Open Space District
Kathryn Purcell, USDA Forest Service, Pacific Southwest Research Station
Mark Stanley, California Department of Forestry and California Oak Mortality Task Force (COMTF*)*

Session Moderators

Barbara Allen-Diaz, UC Berkeley, Environmental Science, Policy and Management
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William Craven, California State Senate, Committee on Natural Resources and Water
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Greg Giusti, UC Cooperative Extension
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Douglas McCreary, UC Cooperative Extension
Beverly Ortiz, CSUEB/Self/EBRPD
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Thomas Scott, University of California, Berkeley
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Bill Tietje, UC Cooperative Extension
Claudia Tyler, UC Santa Barbara

The conference proceedings organizers wish to honor Barrett (Barry) Garrison, a dear friend and fellow oak enthusiast who passed away suddenly and unexpectedly on June 8, 2007, at the age of 48. As a native Californian and a lover of the outdoors, Barry's interest in oaks and commitment to their conservation was deep and long-standing. He worked tirelessly to promote sound oak woodland management and was particularly interested in ensuring that wildlife species associated with California's oak woodlands were protected and enhanced. Though Barry is no longer with us, his passion and commitment to oak woodland conservation will endure. Barry is survived by his wife Catherine Vouchilas and his children Nicole and Christopher.

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Opening Remarks

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Opening Speech for the Sixth California Oak Symposium: Today's Challenges, Tomorrow's Opportunities[1]

Greg Sarris[2]

Welcome to the home of the Southern Pomo and Coast Miwok peoples, known today as the Federated Indians of Graton Rancheria of Southern Sonoma and Marin counties. Welcome to the home of so many oaks. From time immemorial the trees sustained us—body and soul. Two hundred years ago, villages of oaks inhabited our hills and plains, lined our creeks and lakes. They were healthy, diverse. Today less than 10 percent of those ancient natives—the oaks—survive. They have been cut down, removed from the landscape. The survivors are plagued with disease. Not much different from the people who understood and tended them.

Today I understand that you have come here to better understand the oaks, not only so that we can find ways again to tend the magnificent trees but, in doing as much, guarantee their very survival. That of course from my perspective is a good thing. As the old timers said over and over again, "as the oaks live, so do the people; as the oaks go, so go the people."

All perspectives, all points of view, must be considered and, in the end, will be necessary. The native perspective, if there is or ever was such a single, quantifiable phenomena, will not be enough, for example, if for no other reason than the world that may have generated that perspective no longer exists. The water table in our homeland is 200 feet lower than it was at the time of European contact. Flora and fauna—and the human beings—all integral to the oak's well-being are absent from the territory or greatly reduced in number. Over 60,000 acres in Sonoma County are planted in grapes, a crop that, as it is currently being raised, exists at the expense of all other plant species. Oh, lest we focus only locally, there is the problem of global warming.

But I, by no means, wish to be gloomy. We always have two choices, as the great ecologist Gregory Bateson once reminded us, "If we are lemmings going over a cliff, we can walk with the rest and drop off, or we can scream as we go and say 'Hey, there's another way.'" I believe I am speaking to a crowd of screamers. I live for screamers and so do the oaks. So, once again, welcome.

But before I leave you to your business, which, of course, is all of our business, trees and humans, let me just come back to the question of perspectives and points of view. At the risk of simplifying our discussion, it seems to me that the discussions will fall into three larger perspectives—all of which are necessary to survival, ours and the trees.

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[1] An abbreviated version of this paper was presented at the Sixth California Oak Symposium: Today's Challenges, Tomorrow's Opportunities, October 9-12, 2006, Rohnert Park, California.

[2] Tribal Chairman, Federated Indians of Graton Rancheria, 6400 Redwood Drive, Suite 300, Rohnert, CA 94928. e-mail: tribe@gratonrancheria.com.

First, there is the scientific perspective. That is where trees and their various issues and problems are discussed in terms of specific plant communities, all carefully categorized and labeled. Trees are discussed in terms of their biological properties. Diseases are discussed in terms of symptoms and causes; in turn, remedies are suggested addressing the respective symptoms and causes. The trees' relationship to other plant—and animal—communities are defined.

Second, and of course closely related to the first perspective, is what I call the tending perspective. Here, issues of conservation and policy regarding the care and restoration of the trees have the spotlight.

Both of these perspectives I am sure all of you take for granted. No new news here.

The third perspective, that is, a spiritual perspective, is one that does not always surface in either our scientific discussions or policy discussions but, at least from my point of view, must inform both of them. I am not talking about a prayer of a song that I, or anyone else, might give you. Nor am I talking about hugging trees. Trust me, not all of them want to be hugged. And that is the point; humility in the face of the spirit of these trees, all that we do not know and can not see. The old timers said that trees had songs, rules they told the people for their care. In fact, entire human communities were organized around respect for trees. Local people knew songs only for trees in their respective areas. You would not steal because the trees could poison you if you did not know the song. We kept the population down: An entire religion was predicated on the spirit of trees and what we did not know. Trees would turn on the people all people—if forgotten. In sum, trees had great power and demanded respect. They are, after all, bigger and certainly older than us.

We don't know the songs. But we can approach our work these next two days knowing we do not know. That can humble us, force us to consider, once again, in all of our perspectives and discussion, that what we are discussing – the great oaks – have power, and that now, more than ever, we need them as much as they need us. They are Gods, we must not forget.

I would now like you to hear a Coast Miwok prayer. *Words, language the trees listened to and understood so long before English. May the trees hear these words and be happy.* And you, too.

Continue

Stewardship and Land Management

Continue

Public Land Grazing for Private Land Conservation?[1]

Adriana Sulak,[2] Lynn Huntsinger,[2] Sheila Barry,[3] and Larry Forero[4]

Abstract

California ranchers with substantial private oak woodlands sometimes use public lands as an important component of their production cycle. Yet allowed public grazing has declined and is likely to continue to decline. This, combined with intensifying development pressure and land use change, dramatically affects the resource base for ranch operations, which in turn influences landowner management decisions and practices. Such individual decisions have a significant role in shaping California's future landscape. As private rangelands are developed and taken out of production, public lands become a greatly sought after forage resource for livestock operators. Public agencies could dramatically expand their spheres of conservation influence by leveraging these important connections between private oak woodland ranches and their public leases. This scenario is examined in two key areas in California: the central Sierra's oak woodland foothills, and the San Francisco Bay Area's East Bay grassland and hardwood rangelands. In both of these areas, the public manages large and crucial swaths of grazed lands surrounded by privately held oak woodland ranch lands. After conducting more than 50 in-depth interviews over the past six years, we find differences between the two groups of operators in reactions to public forage reductions. In the Sierra foothills seeking replacement forage is a common response, whereas in the Bay Area reducing the herd is the most common reaction to a reduction in allowed public grazing. Nevertheless, in response to a total loss of public grazing more than one-third of both groups feel it is likely they would sell their ranches. When the private acreage attached to these public leases is taken into consideration, this study reveals how public land management decisions affect the risks to California's remaining hardwood range.

Keywords: Conservation, development, land use change, leasing, livestock, permittees, public lands, public land grazing, ranching, rangelands, working landscapes.

Introduction

California's oak woodlands are 82 percent privately owned and, due to their beauty and mild climate, are under severe development pressure (CDF-FRAP 2003). One way to conserve this ecosystem is to work with livestock ranchers, as they own and manage most of it. Unfortunately, livestock ranchers face a myriad of well-documented threats: estate taxes, heirship issues, increasing property taxes, industry economics, loss of infrastructure, conflicts with urban neighbors, fragmentation and development of grazing lands, and an unstable forage base (Anderson and others

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[1] An abbreviated version of this paper was presented at the Sixth California Oak Symposium: Today's Challenges, Tomorrow's Opportunities, October 9-12, 2006, Rohnert Park, California.

[2] Graduate Student and Associate Professor respectively, Department of Environmental Science, Policy and Management, University of California, 137 Mulford Hall #3114, Berkeley, CA 94720. e-mail: sulak@nature.berkeley.edu and buckaroo@nature.berkeley.edu.

[3] Bay Area Natural Resources/Livestock Advisor, University of California Cooperative Extension, 1553 Berger Drive, Bldg 1, San Jose, CA 95112. e-mail: sbarry@ucdavis.edu.

[4] County Director and Livestock Farm Advisor, Shasta County, University of California Cooperative Extension, 1851 Hartnell Ave., Redding, CA 96002. e-mail: lcforero@ucdavis.edu.

2002, Hargreave 1993, Hart 1991, Huntsinger and Hopkinson 1996, Johnson 1998, Liffmann and others 2000, Rowe and others 2001a&b, Smith and Martin 1972, Sulak and Huntsinger 2002a&b, Zollinger and Krannich 2002). This last threat, that of an unstable forage base, is the most direct consequence of land use change and development but also possibly the most over-looked. Methods to mitigate this problem could be a powerful key to oak woodland landscape scale conservation.

The inter-linkage of public lands and private lands within livestock operations is common throughout the west and has been since the first public land management agencies were established. Most Americans are aware that public land grazing occurs on the federal lands across the west, but many people do not realize that it is common on many other types of public lands as well—city, town, utility, and local park lands. Using livestock grazing for vegetation management is accepted and defended by many government agencies, as well as nonprofit organizations, as an integral part of land management. It can be used for fire fuel reduction as well as restoring native plants, promoting biodiversity, and enhancing wildlife habitat, including habitat for special status species (EBMUD 2001, Holecheck and others 2006, Nuzum 2005). Nevertheless, despite much research documenting the benefits of grazing for conservation goals, there is a general public and scientific negativity towards public land grazing due to historical and well-documented years of mismanagement, controversial politics, and conflicts with recreation. Consequently, the use of livestock grazing on public lands has declined in recent decades.

As development pressure increases, land in agriculture declines, individual ranches shrink and dependence on the dwindling amount of grazing land increases. Many ranches have, over time, expanded their forage base and their operations by leasing private as well as public lands. Private leases can be tenuous due to their propensity to be lost to housing developments in many areas, whereas public leases are "protected" and are unlikely to be developed. This dependence on leasing has created a scenario in which the policies and management strategies of these federal, regional, and local public agencies directly affects the private oak woodlands and their owners. This relationship should be capitalized upon to the benefit of private ranch land conservation and California's oak woodlands. Public agencies could dramatically expand their spheres of conservation influence by leveraging these important connections between private oak woodland ranches and their public leases through the lessees. In this paper, we will discuss research conducted over the past six years with grazing permittees and lessees in two different areas within California to reveal these inter-linkages between public and private lands and highlight how this relationship could be used to leverage oak woodland conservation.

Study Area

We focus on two areas in which oak woodland ranch lands are threatened by immense development pressure—California's central Sierra foothills and the San Francisco Bay Area. California's land use history is marked by the Spanish and Mexican land grants, which originally divvied up the lands of the state, and the Gold Rush in 1849. The Gold Rush heralded a huge influx of people and livestock and the tradition of transhumance grazing was established. California's Mediterranean climate encouraged this practice, which is defined by the movement of animals between the lower Sierra foothills and the higher elevation mountain meadows. The mountain meadows stay green when the foothills dry out and turn brown in the spring and summer (*fig. 1,* Rinschede 1984). These high-elevation, summer grazing lands are what were placed under the management of the United States Forest Service at the turn of the century and the inter-linkage of public and private lands began.

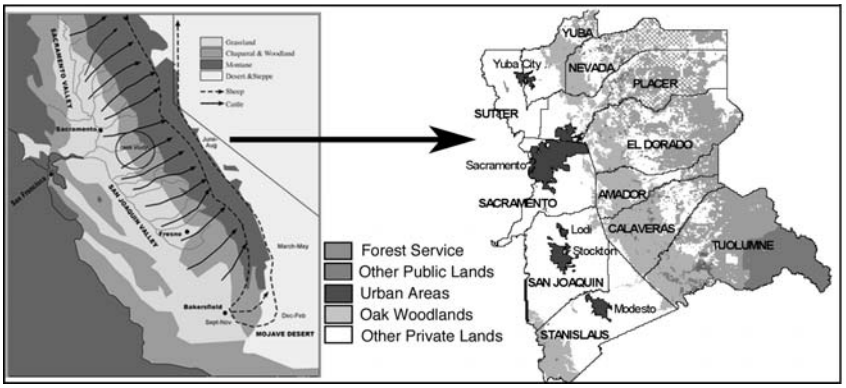

Figure 1—General location map for central Sierra study area and explanation of transhumance in California (Rinschede 1984, CDF-FRAP 2001).

Population growth in the Sierra Foothill study area has boomed since the 1970s and is expected to continue to grow at an exponential rate (*fig. 1*). The Sierra Nevada Alliance, an association of environmental groups active in Sierra-wide conservation issues, estimates that between 1970 and 1990 the population of the counties in the Sierra doubled (Hickey 2005). In El Dorado County specifically, the fastest-growing county within our study area, the population grew by 23 percent between 1990 and 2000 (Hickey 2005). Further, in the western portion of El Dorado County, these demographic and land use changes caused the land used for livestock grazing to decrease from 49 percent of the region in 1930 to 6 percent in 2004 (Wacker and Kelly 2004). Of the ecosystems in the Sierra, the oak woodlands are most under threat. They are home to about 70 percent of the region's population, and less than 1 percent of the foothills are protected from development (Davis and Stoms 1996, SNEP Summary 1996). According to Sierra Nevada Ecosystem Project data published in 1996, 68 percent of Sierra hardwood rangeland is privately owned, almost 2 million acres, but, even then, more than 800,000 acres of oak woodlands in the Sierra had already been converted to other uses (SNEP Summary 1996). The foothill woodlands host the greatest native biodiversity of any of the ecosystem types of the Sierra, and there are 86 species of terrestrial vertebrates that require west-slope foothill oak woodlands for their survival (Graber 1996, Sierra Nevada Ecosystems, SNEP 1996). Overall the Sierra Nevada and its foothills are predominantly federally owned, although the nine counties specifically in our study area are 38 percent publicly owned with individual counties ranging from Tuolumne, which is 76 percent public, to Sutter, which is 3 percent public (CDF-FRAP 2003).

The two counties of focus in the other study area of this research, Alameda and Contra Costa counties, are located in the San Francisco East Bay and stretch from an urbanized shoreline along the Bay on their western edge out through rolling hills of oak woodlands and grasslands towards the Central Valley (*fig. 2*). Land use changes to more intensive agriculture, rural residential, and urban uses have reduced the extent of grazing lands over the years, although on the eastern edges of the counties

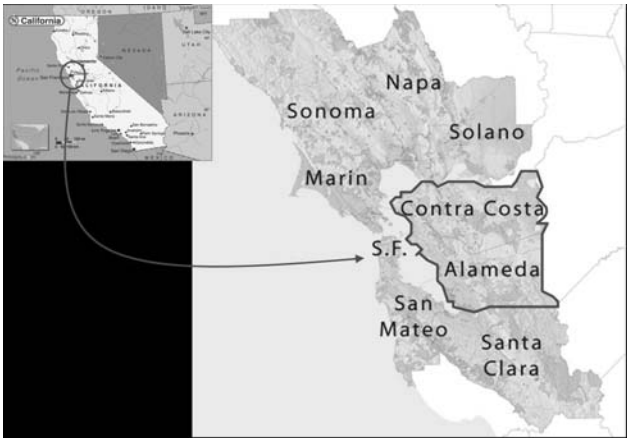

Figure 2—General location map of San Francisco East Bay study area. Colored lands are public (green), or private lands with conservation easements (orange). (Bay Area Open Space Council 2005).

the ranching community persists. Currently, in Alameda and Contra Costa counties, the public owns about 25 percent of the land area (BAOSC 2005), yet almost 40 percent of the two counties is private rangeland and, of the hardwood range specifically, 67 percent is privately owned—about 68,000 acres (CDF-FRAP 2003). These beautiful and productive lands are developing into more intensive uses very quickly and conservation organizations have taken note. In the San Francisco Bay Area, 31 percent of the region's conservation easements are on privately held oak woodland properties (Rissman and others unpublished manuscript). This makes these two study areas at the same time both public and private, urbanizing and rural, as well as ecologically valuable with livestock ranchers controlling much of the remaining oak woodlands.

Methods

We conducted in-depth oral and written interviews of central Sierra ranchers with grazing permits on the Eldorado, Tahoe, and Stanislaus National Forests in 2000 and 2001 (*fig. 1*). This was followed in 2005 and 2006, in a similar interview process, with a group of lessees of three agencies in Alameda and Contra Costa counties: the East Bay Regional Park District, the East Bay Municipal Utility District, and the San Francisco Public Utilities Commission (*fig. 2*).

The central Sierra foothill participants included ranchers with base property in Sutter, Sacramento, Stanislaus, Tuolumne, Calaveras, Amador, El Dorado, Placer and Nevada counties, with some also owning land or leasing outside the study area. Ranchers living further than 150 miles from the study area or to the east of the Sierra crest, and those who were no longer using their permit, were not included, leaving a qualified population of 47 ranchers out of 60 total permittees on the three forests. Twenty-three permittee ranchers completed the survey process. These 23 permittees make up 38 percent of the total population of permittees of the three national forests and about half of the selected population.

The three Alameda and Contra Costa public agencies had 44 cattle lessees between them in 2005. Of those, 33 were selected for the study because they either had an address within the two counties and/or owned land in the two counties. Of those 33, a total of 29 lessees participated in the study. The 29 participants make up 66 percent of the cattle lessees of the three agencies and 88 percent of the selected population.

Data was collected through oral interviews as well as written surveys composed of open-ended, fill–in the blanks, and multiple-choice questions. Some questions reported here were based on surveys created by Helen Rowe and Tom Bartlett for research conducted in Colorado (Rowe and others 2001a&b). In the few instances in which our two case study area responses seemed to be different, comparisons were made using independent-samples “t” tests, and we considered differences of $p \leq .05$ to be significant.

Results

Who is Leasing Public Lands?

The primary interviewees were predominantly male, in their late 50s, and had operations of about 350 brood cows on average, although their herd sizes varied widely (*table 1*). All participants ran cattle, mostly cow/calf operations, although one Forest Service permittee was predominantly a sheep operation. In Alameda/Contra Costa, self-defined combination cow/calf and stocker or yearling operations made up almost half the group, whereas in the central Sierra, permittees considered themselves cow/calf operators while keeping only a very few stockers or yearlings. The two groups’ reliance on family members with off-ranch jobs was similar: 63 percent and 65 percent of the central Sierra and Bay Area groups, respectively, had a family member who worked off the ranch at the time of the interview.

Table 1—*Characteristics of cattle ranchers with public leases in Alameda/Contra Costa counties (A/CC) and the central Sierra (2000 – 2005).*

Characteristic	Participant responses		n	Sig
Percent male	92%		52	
Mean age of interviewee	57 years old		50	
Mean size of cow herd	349 mother cows		41	
Family members with off ranch job	64%		50	
Participation in Williamson Act	83%		41	
	A/CC	**Central Sierra**		
Year began ranching	1885	1907	51	.05
Mean acres owned	4,811	1,904	28	ns

The mean amount of land owned by Alameda/Contra Costa lessee operations is 4,811 acres (sd 11,997, n=18), while central Sierra Forest Service permittees own 1,904 acres (sd 2,387, n=10). However, because of the huge variation in ranch sizes, the two groups are not significantly different (*table 1*). Their public lease sizes are different—the Forest Service average lease size is more than 30,000 acres as compared to a little less than 3,000 acres in the Bay Area due to the difference in natural productivity of each ecosystem. Approximately 83 percent of landowners in the combined group participate in the Williamson Act (a statewide tax relief program and agricultural preserve program). Overall, most of these families began ranching in their areas around 1897, but the Forest Service permittees have been in their area longer, since 1885 on average, and the Bay Area lessees since 1907 on average.

Importance of Leasing

The use of leases, both private and public, allows operations to maintain a herd size that permits a better economic return and provides economies of scale. All but one of the central Sierra Forest Service permittees leased other lands in addition to their federal leases. In the Bay Area, all of the cow/calf lessee operations except two used private leased lands in addition to their public lease and another two operations, which were entirely stocker operations, were completely conducted on the public lease.

In terms of acreage, the Bay Area lessees' operations are an average of 81 percent leased (n=23). Seven operations are conducted entirely on leased lands, both public and private. On the opposite side of the spectrum, one operation whose only lease is public qualified him for the study but makes up only 6 percent of the acres in his operation. That one operation is the exception, however, and if it is removed from the calculation the minimum becomes 41 percent leased and the average increases to 85 percent leased.

In an AUM (animal unit month) based analysis, an average of 18 percent (range of 2 to 45 percent, n=17) of a central Sierra permittee ranch's total forage supply comes from the Forest Service allotment. When asked, "What percentage of your ranch income is attributable to the use of your public lease?" Forest Service permittees and Alameda/Contra Costa lessees reported that the public lease contributed an average of 41 percent and 44 percent to their ranch income, respectively (ns).

In the Alameda/Contra Costa group of lessees, those that used at least one private lease used an average of four different private leases per operation. Four participants did not use any private leases at all, but one rancher used between 10 and 15 private leases each year. The central Sierra group also reported using multiple leases but used fewer, on average about 2.6 per operation (p=.039).

Why Use Public Leases?

Central Sierra Forest Service permittees were asked, "How important to you are the following reasons for using your Forest Service allotment(s)?" "Green feed" was the most important reason for using the Forest Service allotment, with 94 percent of respondents rating it as a "more" or "highly important" reason.

The Alameda/Contra Costa County lessees ranked "location close to other private lands" as their most important reason for using their public lease. Most, or 13 of the 17 landowners who owned ranchlands in Alameda or Contra Costa counties, were adjacent to their public lease or another protected open-space property, and at least five had originally sold their now-leased lands to the public agency. The second most important reason that Bay Area ranchers use their public leases is that there is a "lack of another alternative," and many mentioned during the interview that "the public owns so much land in the two counties" as a reason why public land grazing is so important to the local cattle industry. Similarly, though not quite as strongly, "lack of another alternative" was rated "more" or "highly important" by 84 percent of the participants in the Sierra foothills study area. Although, "lack of another alternative" was rated behind the economic role it played in the operation and also behind the enjoyment of the lifestyle for the Sierra ranchers.

What if Lessees Lose Their Public Leases?

In the written portion of the survey, both groups of participants were asked, “If the public agency that regulates your public lease(s) were to permanently decrease the allowable forage by 25 percent on your public lease(s), what would be your most likely response or responses?” The same question was asked for 50 percent and 100 percent reductions. Compensation strategies choices were described as: 1) “continue” ranching without change; 2) “sell” all or part of your ranch; 3) “stop” ranching but hold on to the ranch; 4) “reduce” your herd; 5) “replace” public land forage with other sources of forage; 6) “diversify” your ranch production; 7) look for off ranch “employment.”

For the 20 landowners in the Alameda/Contra Costa group, any level of change in allowed grazing would result in a parallel reduction in cattle in these operations. “Reduce” was the most popular compensation strategy at the 25 percent and 50 percent reduction levels, and “replacing” the forage was the second most popular. At the 100 percent level, if participants lost their public leases completely, 9 of the 17 lessees that owned land inside Alameda or Contra Costa counties would likely sell all or some of their own land. If these landowners were to lose their leases, a little more than half of them would likely sell all or part of their lands. In comparison, “replacing” the lost forage is the most popular strategy for the central Sierra Forest Service permittees at all reduction levels. Even at the 100 percent reduction level, “replacing” is the most popular hypothesized strategy. Nevertheless, if the Forest Service were to revoke the permit altogether, more than a third of the permittees felt they would likely “sell” all or part of their ranch lands.

Discussion

The preponderance of male interviewees in their late 50s is common to many other studies in California and across the west (Anderson and others 2002, Gentner and Tanaka 2002, Liffmann and others 2000, Rowan and White 1994, Smith and Martin 1972). Concerns about agriculturalists getting older abound, yet they do not seem to age between studies. Their dependence on off-ranch jobs is also true across space and time—with studies originating in the 1970s reporting the role of employment in the local economy as a way to support ranches (Gentner and Tanaka 2002, Smith and Martin 1972). The average size of the operations in this study, though highly variable, is slightly larger than most beef cattle operations across California today but is similar to other studies of public land permittees (Anderson and others 2002, CDF-FRAP 2003, Gentner and Tanaka 2002, USDA Census of Agriculture 2002).

What may surprise researchers and conservationists is the substantial amount of land a California rancher leases to complete the annual forage requirements for a herd of cows. Leasing is important in terms of acres used, AUMs supplied, as well as income generated—all from lands that are not owned or controlled by the operator (Anderson and others 2002, Gentner and Tanaka 2002, Rowan and White 1994). In a California-wide study conducted in 2000 and 2001, researchers found that 88 percent of their sample ranchers owned land as well as leased additional land for their cattle operations (Anderson and others 2002). A survey of 113 Alameda and Contra Costa ranchers in 1993-1994 found 35 percent of respondents used public lands in their operations but unfortunately did not ask about private leasing (Liffmann and others 2000). In our two cases, out of 52 operators, all but three used more leases than their public lease. For the Alameda/Contra Costa group, an average of 80 percent leased acres is an impressive reliance on other people's property.

Land use change in both of these areas has reduced the amount of rangeland available for grazing overall. According to the Farmland Mapping and Monitoring Program, Alameda and Contra Costa counties lost more than 13,000 acres of grazing land between 1994 and 2004 (CDC 2006). The nine-county central Sierra study counties lost more than 34,000 acres of grazing land during the same time period (CDC 2006). These numbers are likely to be much higher because the Farmland Mapping and Monitoring Program does not always include the entire county in its mapping, especially the earlier acreage calculations, and does not include data for Calaveras and Tuolumne counties at all. Hence, regional grazing land is shrinking, and purchasing land locally is unlikely for both groups, which leaves leasing as the main source of forage.

So it seems obvious why cattle operations in these areas would use just about any lease they could find—they must do so in order to have enough land to sustain their operation. But why use public leases in particular, since they have many evident drawbacks? Using public lands, lessees face negative public pressure, deep and slow moving bureaucracies, complex rules and regulations that may run counter to their own management ideas, recreation conflicts, and so on. Their reasons for using public leases differ somewhat due to their location—Forest Service permittees especially value the green feed that the mountain meadows supply. Public lands in the Bay Area are as dry as any other non-irrigated parcel, a function of local geography, and their use is not confined to the summer. Green forage, found in the mountain meadows in the summer when lowland range loses nutritional value, is critical to these operations, and Forest Service permittees often specifically noted that they find summer forage the hardest to replace.

The importance of these leases, and lessee reactions to their hypothesized loss, highlights the opportunity that agencies have to create a more stable local industry and landscape. If one-third to a little over one-half of the participants in each study area is likely to sell all or some of their lands if they lose their public lease, the agencies have an opportunity to influence the fate of their regional landscapes. From our survey, it appears that any reduction in public grazing in Alameda and Contra Costa counties would result in a parallel reduction in the local livestock inventory.

The Bay Area's lessees and livestock industry may be more vulnerable than the central Sierra group, and both of these groups of California ranchers are likely to be more susceptible to changes in public land grazing than their peers in Colorado. In 2001, researchers reported that 26 percent of the 37 federal permittees in their survey would likely sell their land in response to a total loss of their public permit (Rowe and others 2001a&b). The central Sierra ranchers suggested that they are hopeful that "replacing" is possible in their area but similar to the Colorado study, suggested that this may be impossible in reality. For the Alameda/Contra Costa group, the "replace" option never tops the list, an acknowledgement of the impossibility of that compensation strategy. In reality, it is unlikely that even the central Sierra permittees would be able to replace lost permits if the Forest Service changed policy. They, too, have very limited private lands available for grazing and shipping out of state, though common, is expensive.

Both groups lease a lot of land, both public and private, although the public leases seem to be of particular importance. If the public were to revoke grazing leases in these two study areas, there would likely be large shifts from bucolic oak woodlands towards more intensified land uses as the lands are sold. Public agencies could influence landscape stability and management beyond their bureaucratic boarders by working together with lessees. According to respondents, simple improvements in communication as well as general agency appreciation would go a long way. However, if the agencies could take this idea a few steps farther into proactive management and clear intensions for promoting local ranching and working landscapes conservation their influence could be dramatic.

Conclusions

We encourage public agencies to look at how decisions and practices ramify out to the landscape scale, and to think creatively about how they can help their lessees continue to protect their lands from land use change. Through their lessee selection processes, agencies are likely to be choosing the future livestock operators of their area, a role that should be understood and carefully considered. Agencies often depend on private ranches as buffers, and as providers of wildlife habitat for species that roam in and out of private and public lands. An overt appreciation of these connections and their benefits would be ideal, and more transparent, secure and collaborative relationships between agencies and lessees would be a start. Conservation organizations have developed region-wide approaches to conservation, but need to grapple with public-private land interconnectedness. Perhaps one of the most (in)famous examples is in the Arizona borderlands, where the Malpai Borderlands Group has negotiated conservation easements that are linked to state leasing policies (Sayre 2005).

The need of ranchers for more and stable forage supplies is an excellent opportunity for agencies to work with the ranching community. Agency influence through their grazing programs extends the affects of public policy directly to private oak woodland ownership. For example, it has come to our attention that the California Department of Forestry and Fire Protection (CDF) is beginning an initiative to enhance its "vegetation management" efforts in California. However, the vision of grazing for fire hazard management, based on current draft documents (Range Management Advisory Committee to the State Board of Forestry meeting July 7, 2006, Sacramento), is limited to small-scale applications of goats. Cattle, sheep, and other stock also remove fine fuels and can suppress brush encroachment. In light of the problems and costs associated with prescribed burning in the urban-wildland interface, perhaps CDF should think creatively about a convergence of interests between an industry that needs more grass and a fire management agency that wants less of it building up. In this way, agencies could leverage their lands and foster relationships that could conserve their local ranching industry and surrounding landscape.

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Continue

Informing Rangeland Stewardship With Research: Lessons Learned From Yolo County, California[1]

Vance Russell,[2] Chris Rose,[2] and Miles DaPrato[2]

Abstract

Approximately 70 percent of the contiguous United States is in private lands with half of this total in row crop or rangelands. Audubon California's Landowner Stewardship Program engages with farmers and ranchers on conservation and restoration projects in a manner compatible with existing agricultural operations. To assess the success of these efforts, Audubon, University of California, Davis, Agricultural Research Service, and Michigan State University conducted multi-disciplinary studies across a range of habitats in Yolo County, California. We present the results from this multi-disciplinary research as well as highlights of key lessons learned.

Keywords: Oak woodland, private land conservation, restoration.

Introduction

The Willow Slough watershed in Yolo County, California, is an important contributor to the health of the Bay-Delta ecosystem (ERPP 2001). The watershed encompasses the steep eastern slope and low-lying foothills of the inner coast range and the relatively flat alluvial plain of the southern Sacramento Valley. In 1996, the Willow Slough Watershed Integrated Resources Management Plan identified three major categories of natural resource problems within this 131,000-acre watershed, including lack of biodiversity and quality habitat for wildlife as a result of conventional land management practices; degradation of water quality through sediment and nutrient loading; and threats to agricultural sustainability in the region (Jones & Stokes 1996).

In 1998, Audubon-California's Landowner Stewardship Program teamed with the Yolo County Resource Conservation District to implement the recommendations of the Willow Slough Plan throughout the watershed. Conservation actions in the watershed were based upon two assumptions:

1. Successful implementation of conservation and restoration practices is best achieved through a community-based watershed stewardship program with voluntary participation by landowners; and
2. Conservation and restoration practices on individual farms and ranches will increase biodiversity and quality habitat for wildlife, improve water quality, control invasive non-native plants, and sustain the economic conditions for agriculture.

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[1] An abbreviated version of this paper was presented at the Sixth California Oak Symposium: Today's Challenges, Tomorrow's Opportunities, October 9-12, 2006, Rohnert Park, California.

[2] Audubon California Landowner Stewardship Program, 5265 Putah Creek Road, Winters, CA 95694. Correspondence should be directed to lead author at vrussell@audubon.org.

To test these assumptions, we implemented restoration projects, developed a monitoring plan and collaborated with scientists from diverse disciplines to test a series of research questions. Data collected throughout the project provided important land management and conservation information for Audubon. In addition, our findings provided innovative and effective ways for partnering with local farmers on private land conservation projects implemented in a manner compatible with existing agricultural operations.

Research Studies

Our research projects present background descriptions from an analysis of multiple studies that provides synthesis and allows comparison of results across multiple disciplines. Summaries of questions, research objectives, and actions undertaken by collaborators include:

1. **What are the plant and soil responses to restoration of native perennial grasslands?** Researchers hypothesized that rangeland restoration using deep-rooted native perennial grasses will improve grassland ecosystem health and reduce rangeland erosion potential by improving soil water percolation and retention, reducing soil compaction, enhancing nutrient use efficiency, and ensuring vigorous regrowth compared to annual grassland systems (Griffith 2005).
2. **How do grassland and riparian avian communities respond to habitat restoration?** Research objectives were to document the effects of grassland restoration on bird abundance and species composition at upland restoration sites, and to collect baseline data on avian response to riparian restoration to compare with avian use of remnant stands of riparian vegetation (Goerrisen 2005).
3. **What are the forage preferences by livestock to native perennial bunchgrasses versus annual grasses?** Researchers evaluated livestock preferences for annual versus native perennial bunchgrasses as well as measured nutritional quality of both types of grasses (Laca 2005).
4. **What are the correlates of successful native perennial grass establishment, and how can forbs enhance biodiversity in the ecological restoration of annual rangelands?** Two studies examined the correlates of successful upland native perennial grass establishment and the feasibility of using native forbs in grassland restoration to increase biodiversity (Lulow and Young 2005).
5. **Can remotely sensed imagery be used to estimate biomass in rangelands?** Researchers monitored and analyzed biomass dynamics across the watershed; developed methods for remotely detecting different vegetation types; and created a Web-based delivery system to deliver information to stakeholders and inform their range management activities (Malmstrom and Butterfield 2005).
6. **How does vegetation respond to conservation and restoration activities?** Research and monitoring activities included collecting baseline data on plant community composition, measuring vegetation response to restoration activities, establishing monitoring protocols for future long-term data collection and assessing per unit costs of restoration activities (Audubon 2005).

Results

We summarize the results from these six research questions into three broad themes, vegetation response to restoration, avian response to restoration and utility of remote sensing tools to rangeland management, which cut-across the individual studies.

Vegetation Response to Restoration

Monitoring undertaken to determine vegetation response to restoration showed that tree and shrub survival in upper rangeland sites averaged 30 percent with a 24 to 70 percent variation. This average survival, compared to 75 to 80 percent in Audubon valley sites, reflected difficulty of establishment in rangelands largely due to inadequate irrigation (Audubon 2005). In fact, we found that actively managed irrigation at each site led to a significantly higher percentage of survival rates (Audubon 2005). There was variation, however, in the success rate, depending on the species: Blue oak (*Quercus douglasii*), live oak (*Quercus wislizenii*), and foothill pine (*Pinus sabiniana*) had the highest survival rates across all the sites. Use of metal cages to prevent browse and damage from cattle showed a significant increase in survival numbers from 50 to 88 percent, depending on site and species (Audubon 2005).

Control of non-native invasive species was a challenge in many of the research projects undertaken. However, quantitative assessment of medusahead (*Taeniatherum caput-medusae*) relative cover showed drastic reductions from 23 to 36 percent to 0 to 5 percent following prescribed fire. However, data from sites treated in 1999 and 2000 suggested that medusahead may be on the increase three or four years post-fire, even at sites that have been seeded with native perennial grasses and managed with grazing (Audubon 2005). Other studies indicated that early spring prescribed fire may be effective at controlling barbed goat grass (*Aegilops triuncialis*) (DiTomaso and others 2001). In other sites, barbed goat grass cover varied annually, likely responding to other yet to be determined climatic or management variables.

Two studies examined the combined affect of treatments for invasive species (Audubon 2005, Malmstrom and Butterfield 2005). Sites treated with burning or rotational grazing alone showed more variable effects; short-term reductions in weed fractions were evident after prescribed burns, but the effect was not as long-lasting as revegetation (Audubon 2005, Malmstrom and Butterfield 2005). Similarly, the combination of prescribed fire and Transline™ herbicide significantly reduced relative cover of yellow star thistle (*Centaurea solstitialis*) from 6 to 9 percent to 0 to 1 percent.

Determination of biomass production was a component of two out of the six studies. Native perennial grasslands produced more above- and below-ground biomass per unit area and contained higher tissue nitrogen at the growing season’s end (Griffith 2005). Similarly, sites revegetated with perennial species generally exhibited higher above-ground biomass levels in spring and fewer weeds than untreated sites, particularly if the revegetated sites were actively managed with fire or grazing (Malmstrom and Butterfield 2005).

Soil characteristics were a strong determinant of restoration success (Lulow and Young 2005, Griffith 2005). Sites with richer soils can have very high rates of early restoration success (Audubon 2005, Lulow and Young 2005). Native perennial grasslands had higher soil nitrogen fertility, allowed plant roots to absorb more soilbound water (particularly in drought conditions), allowed for more surface water infiltration and minimized erosion on hillsides. (Griffith 2005). One of the most interesting and striking responses that the perennial grassland had on soil properties was the change that occurred in soil water retention characteristics (Griffith 2005). This could be due to the ecological advantage to plants in perennial grasslands by allowing more water to be extracted from the soil under harsh dry soil conditions.

Avian Response to Restoration

Monitoring of avian abundance, diversity and population dynamics is an important tool to measure the performance of restoration sites (Gardali and others 2006). Avian monitoring at grassland sites demonstrated species richness and abundance to be greater in perennial grasslands than annual grasslands with the strongest patterns observed in grassland specialist birds (Goerrisen 2005). Within grasslands with constructed brush piles, nesting by several bird species occurred, as well as avian seed dispersal. Riparian monitoring results showed greater avian species' richness and abundance in mature riparian vegetation sites (Goerrisen 2005). Avian monitoring also occurred at constructed brush piles.

Utility of Remote Sensing Tools to Rangeland Management

Malmstrom and Butterfield (2005) demonstrated that a vegetation classification based on time series of remote-sensing imagery—a multi-temporal analysis—can successfully separate late-season weeds and cool-season forage grasses in project grasslands. Aerial photography proved in many ways to be superior to satellite imagery for vegetation mapping, particularly in terms of its cost, spatial resolution, and the flexibility of scheduling image acquisition. The vegetation classification revealed medusahead and barbed goat grass to be widespread throughout the project watershed. Levels of these two weeds were markedly reduced at several restoration sites, in seeded clover fields and at sites in which we conducted prescribed burns.

Interviews with landowners concluded they would use remote sensing and associated World Wide Web management systems to assist in determining forage dynamics throughout ranches (Butterfield and Malmstrom 2006). The researchers concluded that remote sensing tools would be a cost-effective means to enhance private rangeland conservation (Butterfield and Malmstrom 2006).

Discussion

Research questions have resulted in important findings to further our understanding of restoration in blue oak woodlands. These insights are already being incorporated into conservation and restoration actions throughout the region. Restoration actions implemented with local ranchers with multidisciplinary research projects led to a number of important lessons for working with private landowners.

1. **Collaborate among complementary organizations**—It is well recognized that farming with the wild begins with conservation-minded communities (Imhoff 2003). The conservation partnership between Natural Resources Conservation Service (NRCS), Center for Land-Based Learning, Audubon, and Yolo County Resource Conservation District was critical to the successful implementation and to provide the broad spectrum of technical resources and funding to carry out successful projects.

2. **Develop projects from small to landscape scale**—An unexpected benefit of implementation with landowners was increased habitat connectivity between groups of landowners throughout the watershed. Several researchers have noted the importance of restoration in agricultural areas to native pollinators and other species (Jackson 2005, Maestas and Knight 2003, Kremen 2004). Results from the Audubon studies showed that multiple landowners can be engaged and cooperate in landscape-scale restoration, particularly if it helps to profitably manage forage, weeds and cattle.
3. **Create projects with multiple benefits**—Many of the Audubon-implemented projects had multiple economic and agronomic benefits outside of the intended habitat restoration project objectives. These included improved water quality, reduced soil erosion, flood control and non-native invasive plant control. In general, multiple benefits projects are more appealing to the farm and ranch community due to long-term cost reductions.
4. **Involve students in hands-on restoration projects**—Conducting ecological restoration provides a good opportunity for students to experience hands-on learning. Students participated in many of the restoration projects through planting, installing irrigation, select monitoring activities, and meeting the landowners.
5. **Utilize farmer-to-farmer extension**—Extension or learning between farmers, in addition to learning from experts, has long been recognized as important to technology transfer (Bunch 1982). Creating farmer-to-farmer learning opportunities, formally through workshops and informally through such activities as site visits or field days, engaged more farmers in the program and provided more credible learning opportunities than if Audubon worked on restoration projects individually with farmers. A “bottom up” extension approach allowed us to reach a more diversified group of growers from the large to small and different types of farm operations.
6. **Base projects on resource management plans**—The Willow Slough Watershed Management Plan provided the overall project framework and identified key project needs. Watershed plans often provide the basis for multiple-use projects across many stakeholders and help identify multiple conservation benefits, including agricultural, water, and natural resources.
7. **Provide financial, technical, and logistical assistance for landowners—**The Landowner Stewardship Program was initiated to provide technical and financial assistance to landowners for project implementation. In addition, negotiating the administrative paperwork required by private land conservation programs and regulatory permitting is essential to implement successful projects. Assistance, however, needs to be undertaken in a manner that builds participation and farmer ownership of the process. In this vein, projects must be developed with the landowner’s objectives in mind and integrate in-kind and monetary input from participating landowners.
8. **Test assumptions and measure success**—The research projects described demonstrated the efficacy of treating habitat restoration projects as experiments useful for landowners, researchers and Audubon. However, it is difficult to implement an adaptive management program on three-year funding cycles. Further research is also needed to examine the interactions between restoration projects and agricultural production. Future research for the Landowner

Stewardship Program will be coherently linked through a programmatic science agenda to guide future research and fully assess restoration assumptions. The science agenda will be shared widely with research institutions, conservation organizations, donors, and landowners.

Conclusion

Restoration on agricultural lands is a relatively new field and much still remains to be learned. The projects described in this paper were a first attempt at beginning to understand direct effects of restoration upon biotic and abiotic systems found in Yolo County. Applying research results to management actions in an adaptive management process is not easy, particularly given uncertain funding cycles. Nevertheless, actively testing assumptions made in the field, measuring restoration success and attracting high-caliber research is essential to increasing the credibility and quality of future conservation actions and perhaps public support for the conservation value of farming with the wild.

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Continue

Identifying and Addressing Contemporary Issues in Central Coast Oak Woodlands[1]

Erin Rice,[2] Doug Piirto,[3] Royce Larsen,[4] Bill Tietje,[5] Ryan Cooper,[6] and Ulric Lund[7]

Abstract

Recently, questions about the extent of thinning, the sustainability of forest management practices, and the compatibility with other uses were raised by the media, agency personnel, and environmental groups. In response, University of California Cooperative Extension and Cal Poly San Luis Obispo's Natural Resources Management Department collaborated to address these issues. In March 2006, a questionnaire was mailed to landowners of properties greater than 100 acres in Santa Barbara, San Luis Obispo, and Monterey counties. A total of 2,786 questionnaires were mailed, with 450 completed and returned (16 percent). The respondents were highly educated, holding degrees in areas other than agriculture or natural resources. Most landowners earned degrees in biology, business, education, law, engineering, or medicine. Over 60 percent of respondents were opposed to any county ordinance. However, 71 percent of respondents said oaks are "important" for their aesthetic value, which indicates support for oak protection. Responding landowners feared the loss of private property rights, and felt that government should not interfere with management on private property. Nearly 73 percent of respondents to our survey make less than 25 percent of their income from their land. Landowners rated their knowledge of oak products marketing, laws and regulations (e.g., Forest Practices Act), forest health (e.g., Sudden Oak Death), and available consulting services as especially poor. A majority of landowners who responded to the survey did not know how to get more information on oak woodland management. The workshop presented on August 17, 2006, in San Luis Obispo, was designed to respond to issues and information needs identified by central coast landowners as well as to provide the latest scientific findings and policies regarding oak woodland management.

Keywords: Central coast, contemporary issues, forest management, oak woodlands, survey.

Introduction

Few plants have so greatly influenced a region as the oaks of California's woodlands, which include 18 different species, each with a distinct growth form and physiology. This diversity has allowed the oaks exceptional ecological importance throughout

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[1] An abbreviated version of this paper was presented at the Sixth California Oak Symposium: Today's Challenges, Tomorrow's Opportunities, October 9-12, 2006, Rohnert Park, California.

[2] Student, Natural Resources Management Department, California Polytechnic State University, San Luis Obispo, CA 93407. e-mail: rice.ec@gmail.com.

[3] Professor, Natural Resources Management Department, California Polytechnic State University, San Luis Obispo, CA 93407.

[4] Area Natural Resources Watershed Advisor, University of California, Agriculture and Natural Resources, Cooperative Extension, San Luis Obispo, CA 93407.

[5] Area Natural Resources Specialist, University of California, Agriculture and Natural Resources, Cooperative Extension, San Luis Obispo, CA 93407.

[6] Farm Advisor/Field Assistant, University of California, Agriculture and Natural Resources, Cooperative Extension, San Luis Obispo, CA 93407.

[7] Associate Professor, Statistics Department, California Polytechnic State University, San Luis Obispo, CA 93407.

California's plant communities, including forests, woodlands, and chaparral (Pavlik and others 1991).

The hardwood rangeland occurs in 52 of California's 58 counties, covers approximately 10 million acres, and is held predominantly by private landowners. The central coast counties of Monterey, San Luis Obispo, and Santa Barbara contain a significant portion of the state's total hardwood rangeland and therefore stand out as an important area to study the hardwood resource. Monterey County has 560,000 acres of hardwood forest/woodland, more than any other county in California. San Luis Obispo County has approximately 454,000 acres, and Santa Barbara County has 248,000 acres of hardwood forest/woodland (Standiford and Tinnin 1996). These three counties are among 14 California counties with at least 100,000 acres (Mayer and others 1986).

Since the turn of the 20th century, the relentless population growth in California has resulted in the conversion of many woodlands to accommodate new ranches, farms, and homes. This loss of habitat has not gone unnoticed. Both the botanist Willis Jepson and naturalist John Muir observed the steady loss of oak woodlands in the early 1900s. University researchers, biologists, natural resource managers, and others continue to observe this trend that began to become obvious in the mid-20th century (Pavlik and others 1991).

The Changing Oak Woodlands

Information about oaks is abundant, but its value is limited by how accessible it is to woodland landowners. Making science-based information available to landowners is vital because they will shape the future of California's oak woodlands. Unlike some of the state's other ecosystems, over 80 percent of the total oak woodland is held by private landowners (Giusti and others 2004). These landowners are increasing in number, due to the trend of subdividing ranches into smaller pieces. Subdivision results from high estate taxes, or simply because residential use provides greater economic return than agricultural use. Between 1985 and 1992, 7 percent of the oak woodland was subdivided (Huntsinger and others 1997). Today many more oak woodland landowners are primarily using their land as residences rather than ranches, compared to 50 years ago (Walker and Fortmann 2003).

The result of this subdivision trend is the fragmentation of California's oak woodland ecosystems. The fragmented woodland may appear similar to the native woodland, but many studies have demonstrated that converting to smaller ownerships brings serious ecological consequences, including an increase in invasive plants and decreased numbers of native species, especially birds (Merenlender and others 1998).

Many groups have responded to this threat to the oak woodlands, and policy has been formed to encourage the continued use of oak woodlands for open space or agricultural purposes. The Williamson Act was passed in 1965 to give landowners tax breaks for keeping their land in agricultural use. Constantly evolving estate tax law has been modified to encourage the continued existence of large ranches. Conservation easements are another approach for preserving woodlands. These easements have been developed by land trusts that have formed throughout California in the past 20 years. Easements provide a way to compensate landowners for preserving their woodlands by purchasing the development rights.

Conservation easements have spread in popularity as means for landowners to receive financial benefits without developing their land. These easements have evolved at an extremely fast pace in recent years, making them difficult to understand and regulate (Merenlender and others 2004). A variety of issues related to permitted land use continue to be discussed in relation to conservation easements.

The Project

University of California Cooperative Extension (UCCE) and Cal Poly San Luis Obispo's Natural Resources Management Department acquired funding and began collaborating to address the key issues surrounding oak woodland management in the central coast counties of Monterey, San Luis Obispo, and Santa Barbara. Landowners were surveyed to set up an educational workshop about research and policies to promote good land management decisions.

Previous surveys of oak woodland landowners in California were conducted in 1985, 1992, 1994-95, and 2000-01 (Huntsinger and others 2004). These previous surveys focused on the entire state or on regions outside the central coast area (San Luis Obispo, Santa Barbara, and Monterey counties). The survey conducted here differs because it was designed to outline a workshop while previous surveys focused on characterizing oak woodland owners.

The survey was sent out in March 2006 to identify key issues for the oak woodlands of the central coast, and to assess the need for information by gauging landowner experience and knowledge pertaining to oak woodland management. The workshop was designed to cover issues and information needs that landowners identified in the survey. It is our hope that the results of the survey and workshop will lead to expanded implementation of best management practices in central coast oak woodlands.

Methods

Survey Development

The first set of questions was developed in November 2005. We used Marketing Research (Aaker and others 2001) to design the rating scales listed in the questionnaire. The questionnaire was divided into several major categories, including ownership characteristics, rules/regulations, management practices, products marketing, woodland values, and extended education. The survey went through nine revisions before it was mailed. These revisions focused on improving the rating scales, content, and overall design of the questionnaire.

We originally thought the mailing list could be based on the cattle brand lists from San Luis Obispo, Santa Barbara, and Monterey counties. After some discussion, we decided that the focus of the study should be expanded to include general ownership of the oak woodlands in addition to ranches and farms. Our mailing list was based on GIS parcel data acquired from each of the three counties. We chose to include all parcels of at least 100 acres, which produced a list of roughly 3,000 addresses. In March 2006 the questionnaire, a cover letter required by the Cal Poly Human Subjects Protocol, and a return envelope were mailed to 2,786 landowners.

Survey Analysis

Surveys were returned by 450 of the 2,786 possible respondents (16 percent). The surveys were collected at the UCCE office and immediately separated from their envelopes to ensure anonymity. Due to the anonymous nature of the questionnaire, we believe that some landowners of multiple parcels received more than one questionnaire. Therefore, the true response rate cannot be determined precisely, but is likely somewhat greater than 16 percent.

The response rate was adequate for identifying the interests of likely workshop attendees, but was far too low to make statistical inference about the general population of landowners on the central coast. Nevertheless, we felt it was important to report the results of this survey. The results included in this paper are presented within this context.

Questionnaires were numbered, duplicated, and entered into a Minitab spreadsheet. Additional spreadsheets included a log of comments for question 30 (perceived oak woodland issues) and a spreadsheet to record specified "other" responses for county, land use, degree, work experience, vegetation type, oak products, and information sources. A digital copy of all results was included in the project's final report (Rice 2006).

The results were tallied and used to create pie and bar charts in Minitab. We also used the cross tabulation function of Minitab, along with the chi-square analysis method to test for significant associations between related questions. Responses for some questions were collapsed to facilitate some Chi-square analyses (that is, at least five expected responses for each cell). The results of these Chi-square analyses should be treated with caution and should not be generalized to the larger population of all central coast landowners. Statistical tests were considered significant when $P \leq 0.05$.

Results and Discussion

The results of the survey are presented below in four categories: respondent demographics, attitudes, landowner knowledge, and workshop key topics.

Respondent Demographics

The first section of the survey was focused on demographics. A total of 2,786 surveys were sent, including 1,310 (47 percent) to San Luis Obispo County, 844 (30 percent) to Santa Barbara County, 632 (23 percent) to Monterey County. A total of 450 surveys were returned, including 228 (52 percent) from San Luis Obispo, 123 (28 percent) from Santa Barbara, 81 (18 percent) from Monterey, and 6 (1 percent) from those holding the majority of their land in other counties (*fig. 1*).

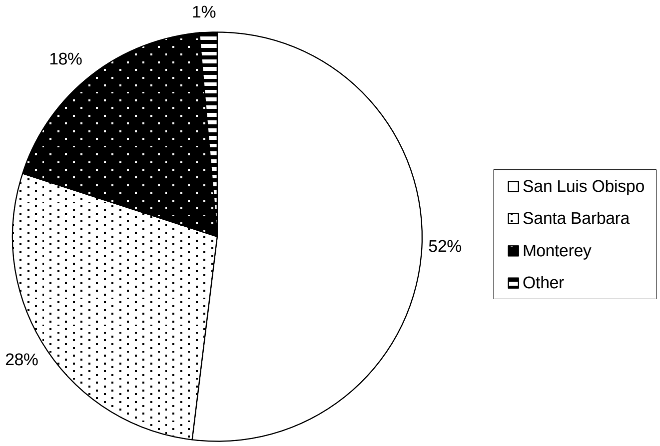

Figure 1—County in which respondents held the majority of their land.

Ninety-seven percent of respondents own their land with only 3 percent leasing. Grazing was reported as the primary land use by 48.5 percent of respondents, followed by crops (14.3 percent), recreation (12.5 percent), and vineyards (9.8 percent). Landowners were asked what percentage of their income was derived from their land. The majority of respondents (73 percent) reported that less than 25 percent of their income was derived from their land (*fig. 2*).

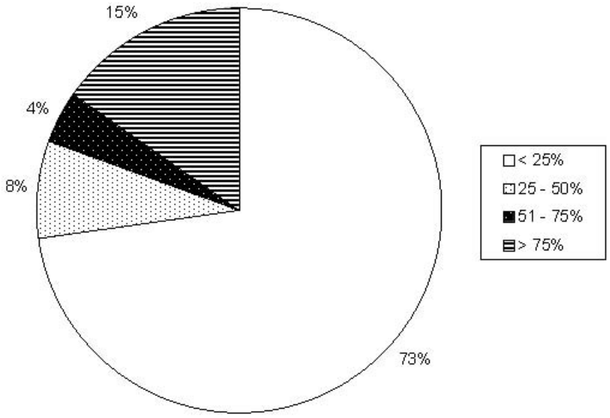

Figure 2—Percentage of income reported as derived from land.

Nearly 40 percent of respondents reported owning their land for more than 30 years, while 14 percent have owned their land for less than 5 years. Nearly 72 percent of respondents plan to keep their land for at least 30 more years.

These associations apply to the survey respondents, but not to the general population of central coast landowners. The majority of these associations depend on how much those who responded to the survey relied on their land as a source of income. The county of residence seemed to influence dependency on woodlands as a source of income, with those in Monterey County earning the greatest share from their land (*table 1*). More highly educated survey respondents earned less of their income from their land. Those who depended more heavily on their land to make a living were more opposed to a county oak woodland ordinance. Respondents who earned less income from their land were more concerned with forest management and forest health issues. Those who were actively marketing forest products reported having more experience with forest treatment methods.

Table 1—*Relationships between survey variables.*

Significant relationship/trend	P-value
County of residence was related to percent income earned from land.	0.027
Education level declined with more income from land.	0.025
Opposition to oak ordinance increased with more income from land.	0.009
Concern for forest management increased with less income from land.	0.027
Concern for forest health increased with less income from land.	0.044
Experience with forest treatment methods was associated with forest products marketing activity.	0.042
Experience with forest products marketing increased with greater forest products marketing activity.	0.000

Over 92 percent of respondents said they had taken at least some college courses, and 74 percent had at least a Bachelor's degree. A significant association exists between a respondent's education level and income earned from the oak woodland. Results suggested that respondent education level decreased as a greater portion of income was earned from the oak woodland. These results seemed to agree with a 1985 survey that suggested that education level decreased as property size increased, and those with larger properties were more likely to sell oak woodland products (Huntsinger 1990).

Our survey also showed that nearly 84 percent of college-educated respondents reported having a degree other than crop science, animal science, or natural resources. Respondents had degrees in biology, business, education, economics, engineering, law, medicine, psychology, etc. This suggests that central coast oak woodlands are being used as residences by many highly educated landowners outside of the traditional agriculture and natural resource fields. Further research will be necessary to confirm this apparent trend.

Over 44 percent of respondents had 0-5 years of experience in managing oak woodlands, and 48 percent did not have experience in farming or ranching.

Evergreen oaks were the most dominant vegetation type, followed by mixed oaks and deciduous oaks. Only 2 percent of respondents did not have oaks on their property. Nearly 63 percent of respondents reported 10 to 20 inches of rain per year on their land.

Attitudes

The respondents to the survey were generally very opposed to a county oak woodland ordinance, and many expressed their opposition to any regulation. Over 60 percent were opposed, 24 percent in favor, and 16 percent were unsure or declined to answer. Many landowners said that they fear the loss of property rights and thought that the government should keep out of oak woodland management of private lands. Previous research (Huntsinger 1990, 1997) found that owners of smaller properties were significantly more likely to believe that oaks woodlands should be regulated and were less likely to sell products from their land. While our survey did not separate landowners by property size, it did find significantly greater opposition from those who earned more income from their land (*table 1*).

Landowner Knowledge

A major portion of the survey asked respondents to rate their own knowledge of certain oak woodland issues (*fig. 3*). They were asked if their knowledge was poor, fair, good, or very good. Many respondents for each question rated themselves as having poor knowledge in several categories. Knowledge of oak products marketing, the Forest Practices Act, Sudden Oak Death, and available consulting services stood out as the poorest categories. Fire/fuels treatment and biological values were the only areas in which poor was not the most common response.

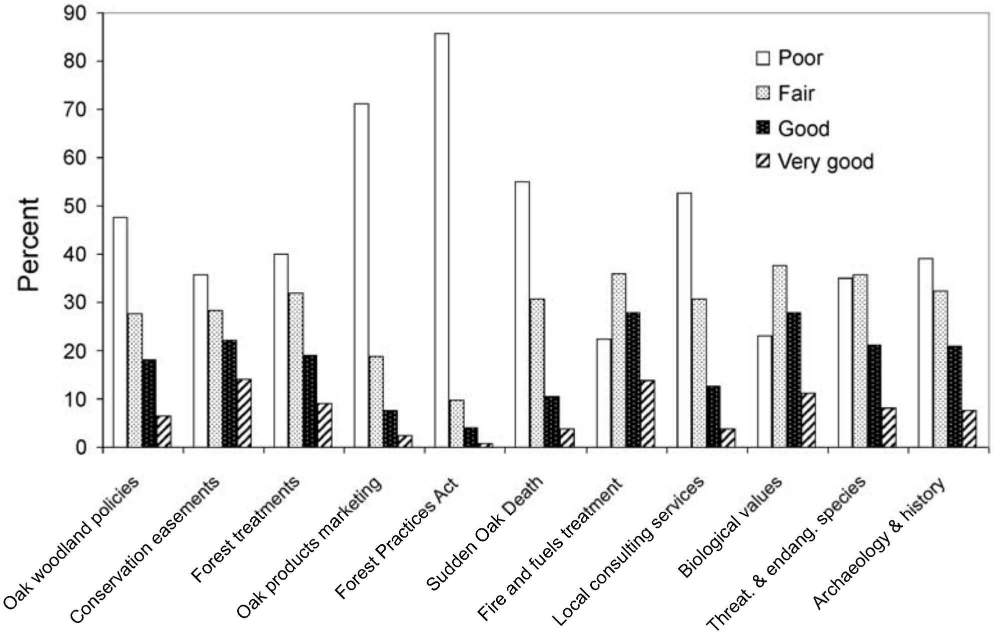

Figure 3—Landowner's evaluation of their knowledge of oak woodland management practices.

Workshop Key Topics

The survey was intended to gauge the need for a workshop about central coast oak woodlands. Landowners were asked if they knew where to get more information and were requested to identify their source. The fact that 63 percent of respondents did not have a source for more information showed that a workshop would not be redundant and could be very beneficial to those seeking to become more knowledgeable. Respondents listed information sources such as University of California Cooperative Extension, Natural Resources Conservation Service, U.S. Department of Agriculture, the California Farm Bureau, California Department of Forestry, Bureau of Land Management, California Oaks Foundation, Cal Poly San Luis Obispo's College of Agriculture, the Internet, and many others.

Landowners were asked for which forest management practices they would like more information. They indicated a desire to learn more about reforestation, understory management, pruning, and thinning (*fig. 4*).

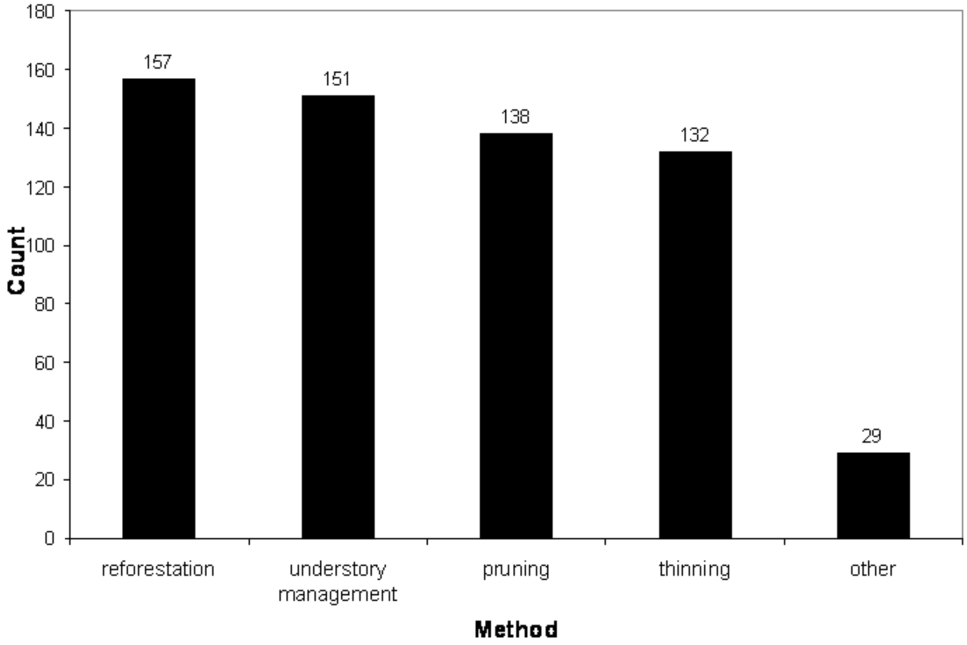

Figure 4—Forest management methods for which landowners indicated they would like more information.

Landowners were also asked which key topics they would like covered in a workshop. Grazing, which was the dominant land use reported by the respondents, was also the most popular key topic (*fig. 5*). Other key topics included regeneration, fire/fuels management, rules/regulations, forest management, and forest health.

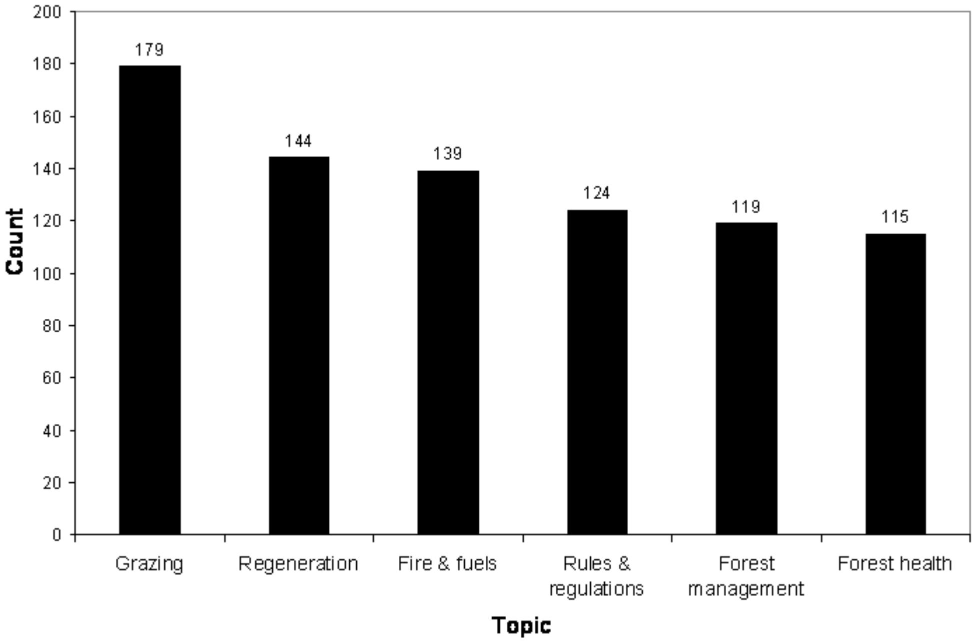

Figure 5—Topic areas landowners indicated they would like covered at the workshop.

Respondents also were given space on the survey to provide general comments on other topics that were not coved by specific questions on the survey. A number of people were concerned about development, urban sprawl, property rights, and education regarding oak woodland management.

Summary and Conclusions

Our 2006 survey had a response rate of 16 percent (450 of 2,786), and focused on identifying contemporary issues and information needs of central coast oak woodland owners (>100 acres).

In the social sciences, the results of surveys with response rates below 70 percent have questionable generalizability to the population of interest. Selection biases for these surveys are likely to be large enough to influence the results and results will diverge from the population of interest (Huntsinger pers. commun.). For this survey it is likely that respondents were generally better educated, and specifically more interested or knowledgeable about oaks, workshops, and environmental issues than those who did not respond.

During this project we learned a great deal about sampling design. To conduct an effective survey of landowners, it is very important to identify the project's objectives prior to budgeting and designing the survey. The number of landowners targeted should be based on how many the project can afford to survey and follow up (there is no reason to sample an entire population). Follow-up (additional mailings, phone calls, etc.) is an extremely important part of achieving a higher response rate. An important reference for designing an effective survey is *Mail and Internet*

Surveys: The Tailored Design Method (Dillman 2000). This method was recently well described and used by researchers conducting a survey in Wisconsin (Clendenning and others 2004). This paper also will serve as a reference for future survey projects.

In the future we hope to conduct another survey of central coast landowners that closely follows this method and provides results that are representative of the general landowner population. Currently, oak ordinances are a major issue on the central coast. Santa Barbara County is struggling to implement its existing ordinance, and San Luis Obispo County has recently received a recommendation from the grand jury to adopt an ordinance of its own. Ordinances already exist in the cities of Atascadero and Paso Robles. For these reasons, we believe it would be valuable to know what the central coast landowners think about oak woodland management issues.

Most respondents to the 2006 survey showed substantial interest in the central coast oak woodlands, and many were enthusiastic about attending a workshop. Some felt that a workshop was unnecessary, but still expressed concern regarding the key issues of the oak woodlands. The majority of respondents generally rated themselves as having “poor” to “fair” knowledge of many important oak woodland issues, and the majority said they do not know where to find more information about oak woodlands.

The interest in oak woodlands and the need for education provided sufficient justification to conduct a workshop. As a result, a workshop was planned and designed based on the characteristics of the landowners who responded, the key issues, and information needs that they identified. The central coast oak woodland workshop was held on Aug. 17, 2006.

Prior research has proven that a fundamental shift has been taking place in the ownership of the oak woodlands. Large ranches are subdivided into smaller properties whose owners do not make a living from their land (Huntsinger and Fortmann 1990). Despite targeting owners of properties larger than 100 acres, our 2006 survey found that nearly 73 percent earn less than 25 percent of their income from the woodland. For this reason, the workshop was not tailored to one group but rather to landowners in general. This broad range of landowners has legitimate concerns about their oaks and desire to improve their management strategies.

The workshop included 10 lectures that were one-half hour each. The topics included a keynote address, 2006 survey results, sustainable forest management, wildlife habitat, grazing, regeneration, rules/regulations, disease/insects, and wood products. The theme of sustainability was present throughout the workshop. The workshop was well received as evidenced by the evaluations returned by workshop participants.

While we are excited about sharing our results with other oak researchers, we conducted this project with central coast landowners in mind. This project aims to support the Integrated Hardwood Range Management Program in its mission to conserve California's hardwood rangeland. This paper provides information about the landowners who are most likely to attend natural resources extension workshops. We believe empowering landowners with knowledge is a crucial part of achieving this goal. We have focused on the central coast because it is one of the key oak woodland regions of California. Our hope for this project is that it will promote informed land management decisions that contribute to the conservation of the central coast's oak woodlands.

Acknowledgments

We thank UC Cooperative Extension for funding this project. We greatly appreciate Dr. James Ahern's input on the survey's design. Acknowledgement is given to Dr. Lynn Huntsinger and Dr. Tim Plumb for providing reference information. We wish to thank those who participated in the Oak Woodland Management Workshop: Dr. Doug McCreary, Eric Huff, Dr. Wally Mark, Larry Bonner, and Dr. John Shelly. Their efforts were well received and greatly appreciated by those who attended the workshop. We wish to thank two anonymous reviewers and Kathryn Purcell, who reviewed this paper prior to the symposium. Their valuable input greatly improved the focus of this paper. We also thank Ms. Sherry Cooper for facilitating our participation in the symposium.

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Continue

Contemporary California Indians, Oaks, and Sudden Oak Death (*Phytophthora ramorum*)[1]

Beverly R. Ortiz[2]

Abstract

This paper begins with a survey of contemporary California Indian utilization of acorns for food, including an examination of: (1) familial, community and cultural contexts in which acorn is shared and eaten; (2) new and old acorn processing techniques in use today and the foods that result; (3) the symbolic context of the foods in terms of ecological and social relationships that connect people to place, each other, cultural heritage and sacred time; and (4) ancestral burning and pruning techniques used to manage oaks and other species. Next comes a detailed summary of contemporary uses by California Indians of plant species affected by Sudden Oak Death (*Phytophthora ramorum*). An overview follows of the impact that Sudden Oak Death (SOD) has had in disrupting, limiting, and sometimes severing the eons-old relationships that California Indians had with the affected species. The paper concludes with a synopsis of how California Indians are responding to this threat to cultural continuance.

Keywords: Acorn, California Indians, land management, oak, tanoak, Sudden Oak Death.

Introduction

Hundreds of publications, both scholarly and popular, have described and otherwise discussed the use of acorns for foods by California Indians, but most people remain unaware of the continuing importance of these foods for contemporary California Indians culturally, socially, and spiritually. This paper will contextualize that use, elaborating on the tangible contexts (present-day processing techniques) and intangible contexts (social and spiritual) that inspire its making. It will also contextualize the use of fire and pruning by California Indians to manage oaks and other plant species past to present.

While the use of "acorn" for food has survived more than 200 years of severe cultural disruption, upheaval, dislocation, and suffering as a result of non-Indian intrusion, it now faces a new threat—Sudden Oak Death (*Phytophthora ramorum*), or SOD. As of September 11, 2006, 23 native plant species and one genera have been designated as regulated hosts for SOD, and 18 other associated native plant species may soon follow. This paper will end with an examination of contemporary California Indian uses of these species, including the most important acorn-producing species for food statewide, as well as numerous other species used today for food, medicine, ceremony, fishing, hunting, cooking implements, and more; and the response of California Indians to the spread of SOD.

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[1] An abbreviated version of this paper was presented at the Sixth California Oak Symposium: Today's Challenges, Tomorrow's Opportunities, October 9-12, 2006, Rohnert Park, California.

[2] Graduate Student, Department of Anthropology, University of California, Berkeley; Lecturer, Department of Anthropology, California State University, East Bay, beverly.ortiz@csueastbay.edu; Naturalist, East Bay Regional Park District, Coyote Hills Regional Park, bortiz@ebparks.org.

Methods

The information about contemporary California Indian plant uses elaborated in this paper is the result of 30 years of qualitative, anthropological field research conducted in collaboration with hundreds of California Indians statewide in both private and public settings.

Emphasis is placed on plant uses in those areas currently affected by SOD, although uses in other areas have been included, given the widespread importance of acorns as food, as well as the fact that contemporary California Indians may gather from plants growing anywhere that is available to them, not solely within their tribal territory.

The goal of this paper is to broaden awareness of the continuing importance of woodland and other natural resources for contemporary California Indians and to provide another framework through which to consider the impacts of SOD and how to respond to it.

Karuk cultural consultant Kathy McCovey aptly encapsulated the cultural importance of oaks and other species when she explained in 1998, “The Spirit People told us...how we were supposed to behave and what we were supposed to do... It’s a holistic way of looking at things [without] a beginning and end... It’s gathering acorns, gathering mushrooms, gathering pepperwood nuts, gathering basket materials all year long... It’s a process that we keep going through.

“People need to know about our lifestyle, the plants we use, and that the Indian culture is alive and well and thriving, and getting stronger every day.”

Or, put another way by Kathy in 2003, “We subsist upon the forest. The forest is us, and we are the forest and the animals within.”

The Use of Acorns for Food Today[3]

As for countless generations, California Indians continue to utilize acorns for food today. Strong memories remain of acorn processing techniques used by a respected elder relative, a grandmother, mother, aunt, or someone else. These memories continue to inspire. People eat “acorn,” as they commonly call the resultant foods today, when alone. They share it during family meals, give it as gifts when visiting friends, and prepare it for special occasions, such as reunions and “big times,” large gatherings that feature ceremonies, feasts, and gambling tournaments.

While some people still make acorn with the old techniques, most people lack the necessary baskets and wooden implements. Instead, they use new methods that creatively blend past and present in an astonishing diversity of methods, the nuances of which vary from group to group, family to family, cook to cook.

Burlap sacks, plastic-mesh sacks, and cardboard boxes have replaced the burden baskets[4] of old among contemporary gatherers. They load these into cars and trucks for the trip home.

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[3] Unless otherwise indicated, all information about acorn use is derived from field research conducted from 1976 to present. Some of this information has been published by the author in the following: Ortiz 1989, 1990, 1991, 1991b, 1991c, 1996/97, 2000, 2000a, and 2004.

[4] California Indians used such cone-shaped baskets to carry loads. They suspended the baskets against their backs in nets. The nets had a cordage strap that wrapped across the forehead.

To prevent mold, people dry acorns on cloth, cots, and specially built, wire-mesh "tables," and in boxes, often placed near or beneath wood-burning stoves and heaters—whatever will work. Once dried, they commonly store acorns in boxes, sacks and jars; again, whatever will work. Stones and hammers are widely used to shell acorns. Instead of using winnowing baskets, people use knives to scrape away the red skins that adhere to some species' nutmeats, or rub the kernels between their hands.

Such alternatives have evolved over decades, some dating to the 1800s. Hand-crank grinders began to replace pounding rocks early on. These were adapted to run on gas, then electricity. Blenders, coffee grinders and food mills have more recently replaced the pounding rocks (mortars and pestles) of old, supplemented when needed by wire-mesh flour sifters in lieu of sifting baskets to separate the coarse particles of acorn from the fine.

For leaching the bitterness (tannic acid) from the acorn flour, people have long placed loosely woven, cotton cloths atop outdoor sand leaching basins. At times, these cloth-covered basins have been modernized still further by being placed atop a wire-mesh screen attached to a wooden framework and supported a few feet above the ground. Pine needles and leaves sometimes substitute for sand. Indoors, contemporary leaching methods include placing acorn flour atop a cloth-covered winnowing basket, imported basket, colander or strainer perched in the kitchen sink below the faucet. People sometimes also wrap acorn flour in loose-weave, cotton cloth and tie this to a kitchen faucet so water can drip through the flour during the night.

For cooking, stainless steel pots on stovetops have largely replaced baskets and heated stones. The use of cooking baskets and stones has increased in recent years, as has the weaving of the baskets, although African-made coiled baskets are sometimes substituted. When baking acorn bread in pit ovens, a rarity compared to the multiplicity of soups and mushes made today, the older method of wrapping the bread with particular species of leaves and fronds is combined with the newer method of wrapping it in wet cloth.

At times, California Indians store acorn flour, unleached or leached, in refrigerators and freezers, cooking it later. Once cooked, soups and mushes may be stored in refrigerators and freezers, or canned.

Whatever the method chosen, old or new, the food remains to provide sustenance, enjoyment, memories, and an important expression of heritage.

Symbolic Content of the Food

"Woodland areas are alive. The plants, the animals, insects, everything has a living spirit, and we need to respect those things."

--Eric Wilder (Kashaya Pomo) 2006

The logistics of creating food from acorns masks a much deeper cultural significance to the food, which continues to inspire its making, despite lack of necessity. It is harder to obtain acorns today than in the past. Many gathering places "owned" by individuals, families, or groups for as long as anyone can remember are now off limits because of private property restrictions and modern laws. Treasured oaks and tanoaks have also been cut down to make way for developments.

Even with the difficulties, many California Indians still find a way to gather, knowing that the interaction between themselves and the trees is an important one in which both are nourished. As Julia Parker (Kashaya Pomo/Coast Miwok) learned from Yosemite Miwok/Paiute people, “The elders told me when it comes get out and pick and gather, even if it’s one basketful, so the acorn spirit will know you’re happy for the acorn, and next year the acorn will come” (Ortiz 1991c: 41).

This belief—that the earth and sky and all objects in between have life and consciousness—underpins the spiritual traditions of indigenous people throughout North America. The world has the potential for both good and bad, not in the moral or ethical sense of right and wrong, but as an expression of harmonious and inharmonious elements. People keep the world harmonious (balanced) through prayerful thoughts, actions, and offerings, adherence to rules of proper behavior, and the observance of spiritual dances in proper seasons on a yearly cycle (Bean and Vane 1978). These spiritual practices likewise underpin traditionalist California Indian interactions with oaks, tanoaks, and acorns today. For instance, traditionalist Miwok/Paiute and those they have taught refrain from wishing for acorns or looking at them in the trees lest the acorns be scared away and a poor harvest result. Prayers occur during acorn gathering and the preparation and sharing of the food, with some of the food offered to the cooking fire before eating (Ortiz 1991c: 38-39).

Ceremonial dances may be thought of as a visible prayer (Bates 1982). They provide a means to thank the Creator. They serve to renew the world, maintain its spiritual balance, and insure the health and well-being of the group (Bean and Vane 1978).

Every autumn, several Central California tribes host “big times” to dedicate, give thanks for, and celebrate the new acorn harvest. As Julia explains, “When the acorn does come, there’s dances and songs. Take from the earth and say please. Give back to the earth and say thank you” (Ortiz 1991c: 27).

Prayers, offerings, ceremonies and cultural proscriptions provide a tangible means to give back for what is taken. They serve to bind the relationship between people, the plants, the food and “sacred time,” when the world had its birth. The dances recapitulate sacred time, while myth encapsulates it, explaining how people and the world came to be, including foods, such as acorn, and how to prepare those foods (for examples of mythology, see Barrett 1933: 84-85; Gayton and Newman 1940: 28; Goddard 1909: 183-188; Kroeber 1932: 305; Simpson 1977: 13-35).

Fire Management and Pruning[5]

Contrary to the image of California Indians as hunter-gatherers with little impact on the landscape they inhabited, they re-shaped the landscape through the use of such horticultural techniques as burning, digging, and pruning. The proper application of these techniques resulted in a world adorned by a complex mosaic of plant communities. This managed landscape nurtured the health and vigor of diverse plant species, while amply providing for the needs of humans and other animal species, including the many species upon which humans depended.

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[5] Unless otherwise indicated, this overview of California Indian land management techniques is derived from field research conducted by the author from 1981 to present. Some of this information has been published by the author in the following: Ortiz 1992, 1993, 1998. For more information about this topic, see Blackburn and Anderson 1993, and Anderson 2005.

California Indians used fire as a management technique to enhance the growth of seed-bearing forbs and grasses, keep meadows open, ensure the growth of mature, open woodland trees with a dispersed understory, and to control some disease organisms and insect infestations. They used it to stimulate the growth of fine, straight, supple shoots used for weaving baskets, and long, straight, sturdy hardwood branches useful for digging sticks and other tools. They also used it to generate the tender, new growth consumed by foraging animals, which, in turn, the men hunted.

In 1792, British Naval Captain George Vancouver described managed oak woodland landscapes as he traveled from Mission Dolores in San Francisco to Mission Santa Clara. About the California coast range, he wrote, "...their sides and summits exhibited a high degree of luxuriant fertility, interspersed with copses of various forms and magnitude, verdant open spaces, and enriched with stately forest trees of different descriptions."

Referring to the route he followed, Vancouver continued, "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 underwood that had probably attended its early growth had the appearance of having been cleared away and had left the stately lords of the forest in complete possession of the soil, which was covered with luxuriant herbage and beautifully diversified with pleasing eminencies and valleys" (Paddison 1999: 84-86).

In 1997, 92-year-old Karuk elder Ramona Starritt described the fire-managed landscape of the Trinity River area that she grew up in, "The Indians burned all over... The earlier years it would just burn, burn, burn, until the sun looked like a big orange. It just burned itself out. That was that.

"They did it for the purpose of their basket weaving, and for the animals. The deer had to eat. They ate the young sprouts. And you could see for miles. You weren't hemmed in with brush... There were very nice trees. You go to where the Indians lived and burned, you'll see really tall fir trees; and pine trees, and madrone trees were large... When I was young, you could see clear across the gorge. You could look over, see a bear climbing the mountain, or a deer, or anything."

Photographs taken in the Trinity River area in the late 1800s and early 1900s provide visual documentation of the same (McCovey 2003).

California Indians managed several species of oaks and tanoak with fire and pruning. The Pomo managed Oregon oak, valley oak, and tanoak stands with fire, while the Northfork Mono and Chukchansi/Choynumni used fall burns to manage black oak (Anderson 2005: 138; Peri and others 1985: 81, 82). The Karuk, Yurok and Hupa likewise managed oaks with fire. According to Kathy Wallace (Karuk/Yurok/Hoopa 2003), "I was told...they would burn under oaks, and it took care of a lot of the bugs... It was a low-temperature burn, but it would take care of ground-carried diseases. It would also clear off the area underneath the trees to make it easier to gather the acorns."

Other northwest California accounts of oak management credit it with hastening the acorn drop, and burning up old acorns, duff and decaying wood and bark that would otherwise become host to a new generation of filbert worms, filbert weevils, their pupae and other insect pests the following year. As with Vancouver's account, ground burning likewise kept mature oaks well spaced and free of tall understory. In addition to these benefits, the Maidu noted oak savannahs as easier to travel through and spot game and enemies. Forbs, grasses, bulbs, corms, and tubers likewise had more space and light to grow. Ground fires stimulated root crown sprouting, creating shoots useful for making such implements as shinny bones and digging sticks, depending on the diameter. Fire may also have created conditions suitable for some oak regeneration (Anderson 2006: 145-148, 279, 287-290, 352).

The Pomo, Yosemite Miwok/Paiute and Mono pruned the acorn-bearing tips of oak branches (Anderson 2006:139; Peri and others 1985:81, 82) to increase future acorn harvests. Peri and others (1985: 81, 82) have identified black oak, canyon live oak (*Quercus chrysolepis*), coast live oak (*Q. agrifolia*), interior live oak (*Q. wislizenii*), Oregon oak (*Q. garryana*), scrub oak (*Q. dumosa*), valley oak (*Q. lobata*), and tanoak as all having been pruned, in the case of scrub oak for straight, flexible shoots useful for basketry.

Today, California Indians across the state, with the support of their tribes, and local basketweavers[6] and other organizations, are working with land managers to bring fire back to the landscape in the form of prescribed burning for cultural purposes, and the concomitant health of the environment. They have made particular strides in working with the United States Department of Agriculture Forest Service in northwest California to conduct burns for beargrass for basketry, as well as with private landowners for hazel burns for basketry. The Hoopa Valley Tribe, with its large landbase, has conducted several cultural burns in recent years. California Indian graduate students have conducted, and are in the process of conducting, M.A. and Ph.D. studies to quantify the effect of burning on particular plants. This includes Don Hankins' (Plains Miwok/Osage) Ph.D. study of pyrogeography (Hankins 2005), Erin Rentz's (Karuk/Yurok) Master's study of cellular changes in northwest California basketry plants after burning (Rentz 2003); and Frank K. Lake's (Karuk) study of how traditional ecological knowledge can be integrated with science to come to a better understanding of northwest California Indian management of sandbar willow for basketry, for which he received a 2005 Community Forestry Research Fellowship.

Longitudinal, quantitative studies of Native-American land management practices in large land areas have yet to be done.

Sudden Oak Death

"Invasions have had a huge impact on our culture, from the settlers who came in, right down to the microscopic level of different [pathogens], such as smallpox, that have come in... "

--Don Hankins (Plains Miwok) 2003

Since July of 2000, when researchers identified SOD as the cause of unusual levels of tanoak die offs in Mill Valley, Santa Cruz, and Monterey, California Indians have had to grapple with a new and wide-ranging threat to cultural survival. Not only does this disease kill particular species of acorn-producing trees, but two of those species, black oak and tanoak, are the most valued acorn-producing species used by California Indians statewide today. As Karuk cultural consultant LaVerne Glaze (2003) explained about the prominence of tanoak acorns as a contemporary dietary staple, "I can see different ones [in the fall] out there all the time trying to find them."

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[6] For example, Karuk Indigenous Basketweavers, Southern California Indian Basketweavers Organization, and the statewide California Indian Basketweavers Association.

Of the 23 native plant species and one genera that have been designated as regulated hosts for SOD as of September 11, 2006,[7] and the 18 other associated native plant species that may soon follow as regulated hosts, the author has identified contemporary cultural uses for all but 12. This does not mean, of course, that those 12 lack contemporary cultural uses, but only that such uses have not been identified. Additional, as yet unidentified, cultural uses may also exist for the others.

Although outside the scope of the present paper, it should be noted that Robert Clement (2006), Plant Protection and Quarantine Technician for the United States Department of Agriculture in Morgan Hill, California, has compiled 39 fact sheets based on data related to past uses by California Indians of 42 species "that are in some way associated with SOD," and/or their California Indian names or poisonous qualities.

A summary of contemporary California Indian cultural uses of regulated hosts and associated native species in Northwest (NW) and Central (C) California follows in table form.

Regulated Hosts	
Acer macrophyllum	**Big leaf maple**
NW: Stripped inner bark used to make girls' and women's work skirts (Colegrove 2006, McCovey 2006, Ortiz 1996/97: 28, 29).[8] NW/C: Leaves used for wrapping bulbs, corms, deer meat and other foods baked in pit ovens.[9] C: Maple shoots from winter coppiced, pruned or burned plants heated, then split four ways; used as overlay in twined Maidu baskets and as sewing strands in Maidu and Sierra Mewuk coiled baskets (Ortiz 2000/01: 8-9).[10]	
Adiantum aleuticum	**Five-fingered fern** **Western maidenhair fern**[11]
NW: Dried or fresh leaves gathered before the spores form steeped in boiled water to make hair rinse (Ortiz and others 2006: 123). Black half of stem used as design overlay in finely woven baskets (Ortiz 1996/97: 27, 1998: 26).	
Adiantum jordanii	**California maidenhair fern**
NW: Dried or fresh leaves gathered before the spores form and steeped in boiled water to make hair rinse; applied after shampooing to soften hair. A teaspoon of leaves steeped in a cup of boiled water to treat fevers; the resultant tea taken two to three times a day until fever gone. Caution: Some people are allergic to the tea (Ortiz 1998, Ortiz and others 2006: 124).	

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[7] The list of regulated hosts and associated plant species given in this paper comes from the California Oak Mortality Task Force web site, http://nature.berkeley.edu/comtf.

[8] Field data 1997 to 2006.

[9] Field data 1980 to 2006.

[10] Field data 1981 to 2006.

[11] Although this plant is usually referred to as five-fingered fern, northwest California Indian basketweavers refer to it as maidenhair fern.

Aesculus californica — **California buckeye**

C: Nuts processed into mush and served with pit oven-cooked deer meat, seafood, roasted peppernuts, and contemporary picnic foods within the living memory of Kashaya Pomo individuals (Ortiz 1989a: 25)

Arbutus menziesii — **Madrone**

NW: One teaspoon of chopped bark slab steeped in cup of boiled water taken three times per day to reduce blood sugar (Ortiz and others 2006: 166). Dried berries pounded, then water added to make a sweet drink. Fresh leaves rubbed and placed on cut to help blood coagulate (McCovey 2006). C: Differently shaped and colored leaves used to represent people and their cultural roles during game played by Kashaya Pomo girls (within living memory) (Ortiz 1994: 42-45). Like oak, this hardwood preferred for pit-oven cooking (Ortiz 1989a: 26).

Arctostaphylos manzanita — **Parry manzanita/Manzanita**

NW: Powdered berries of *Arctostaphylos manzanita* or greenleaf manzanita (*A. patula*) soaked in water to make a sweet cider. Ashes made into paste and poulticed on burns. Leaves boiled in water to make a strong wash used to relieve the itch of poison oak rash. Half teaspoon of leaves steeped in a cup of boiled water and taken three times a day for stomach flu (Ortiz 1996/97: 27, Ortiz and others 2006: 63, 167-168). Wood burned to make hot coals (McCovey 2006). Coals used for cooking and ceremonial fires (Colegrove 2006, Glaze 2003). Coals especially good for roasting salmon strips on redwood stakes, grilling eel and barbecuing deer meat, because they do not produce ash that could blow onto the food (Colegrove 2006, Ortiz 1999: 18). This clean-burning wood also used for wood-burning stove fires (Glaze 2003). Wood used for pipe stems (Ortiz 1990/91: 13, 1993/94:20). Wood used as element of ceremonial regalia (Colegrove 2006). C: Water dripped through powdered berries, or powdered berries wrapped in cloth and soaked in water, to make sweet cider. Wood used as element of ceremonial regalia.[12] Wood used by Auberry Mono secondarily to oak for cooking fires used to heat cooking stones (Ortiz 1989: 24).

Frangula californica — **California coffeeberry**
(=Rhamnus californica)

No contemporary uses identified to date.

Frangula purshiana — **Cascara**
(=Rhmanus purshiana)

NW: Leaves, stems, and bark used as a laxative and liver cleanser (Ortiz and others 2006: 96). S: Medicinal tea for stomachaches (Ortiz 1991a: 33).

Heteromeles arbutifolia — **Toyon**

NW: Berries roasted for food for childhood entertainment by holding branch over fire (within living memory) (Ortiz and others 2006: 248).

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[12] Field data 1980 to 2006.

<table>
<tr><td><i>Lithocarpus densiflorus</i></td><td>Tanoak</td></tr>
<tr><td colspan="2">NW: Acorns preferred for food. The “old timers” relished garnishing their acorn with roasted peppernut halves. Paste from unleached acorn flour or bark ashes used to poultice burns. Water containing acorn flour leachate used to treat eye infections and cataracts. Tanoak mushrooms for food and to lower blood pressure (Ortiz 2000a: 32, Ortiz and others 2006: 42, 49, 52, 66-68, 70, 184-185, 242-243).[13] C: Acorns preferred for food by Pomo and Ohlone peoples.[14] Like oak, this hardwood preferred for pit-oven cooking (Ortiz 1989a: 26).</td></tr>
<tr><td><i>Lonicera hispidula</i></td><td>California honeysuckle</td></tr>
<tr><td colspan="2">No contemporary uses identified to date.</td></tr>
<tr><td><i>Maianthemum racemosum</i>
<i>(=Smiliacina racemosum)</i></td><td>False Solomon’s seal
Fat Solomon’s seal</td></tr>
<tr><td colspan="2">NW: Bulbs and berries used as sedative during labor. Juice used to prevent poison oak rash, heal bruised or broken bones, and draw out black and blue marks caused by blood beneath the skin (Ortiz and others 2006: 232). Flowers picked by children, who enjoy the sweet taste of the nectar at the base of the blossoms (Colegrove 2006).</td></tr>
<tr><td><i>Pseudotsuga menziesii</i></td><td>Douglas fir</td></tr>
<tr><td colspan="2">NW: New-growth needles used to make a gargle for treating tonsillitis (Ortiz and others 2006: 126). Needles a component of tea taken when relative passes away. Fine, long branchlets with little taper used as warp in fine baskets, especially basket caps (Colegrove 2006, McCovey 2006, Ortiz and others 2006: 126). Saplings some 15 to 20 feet long used for dip net poles and the horizontal brace that supports them (Colegrove 2006, Ortiz 1999a: 19, 1999/00a: 34, Spinks 2006). C: Bark-covered and debarked branchlets fashioned by Mountain Maidu individuals into interconnected rings for decorative necklaces, skirts and chains. New, springtime shoots edible (Ortiz 2000/01: 7).[15]</td></tr>
<tr><td><i>Quercus agrifolia</i></td><td>Coast live oak</td></tr>
<tr><td colspan="2">NW: Curving, lower limbs of the closely-related interior live oak used to connect Douglas fir dip net poles (Spinks 2006). C: Nuts used for acorn making.[16] Wood used to produce hot coals for pit-oven, deer meat cooking (Ortiz 1989a: 26).</td></tr>
<tr><td><i>Quercus chrysolepis</i></td><td>Canyon live oak</td></tr>
<tr><td colspan="2">NW: Paste from unleached acorn flour or bark ashes used to poultice burns. Water containing acorn flour leachate used to treat eye infections and cataracts (Ortiz and others 2006: 42, 49, 52, 184-185). New-growth, lower limbs (long, droopy and curving) that hang over rocks and cliffs along rivers used to make dip-net hoops. Not only is the wood limber, and thus resistant to breakage, but relatively buoyant, staying high in the water. These are lashed to two Douglas fir poles. Other hardwoods used secondarily for the hoops (Colegrove 2006, Ortiz 1999a: 19, 1999/00a: 34, Spinks 2006).</td></tr>
</table>

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[13] Field data 1997 to 2006.
[14] Field data 1983 to 2006.
[15] Field data 1976 to 2000.
[16] Field data 1988 to 1992.

Quercus kelloggii	**California black oak**
NW: Paste from unleached flour or bark ashes used to poultice burns. Water containing acorn flour leachate used to treat eye infections and cataracts (Ortiz and others 2006: 42, 49, 52, 184-185). C: Acorns preferred for food due to their storage capability, thickening properties, color and flavor (Ortiz 1991c:39). Wood used to make fires for heating cooking stones and to produce hot coals for pit-oven, deer meat cooking (Ortiz 1991c: 114). Pruned sprouts bent with heat and water into looped stirrers for cooking acorn with heated stones in baskets (Ortiz 1989:24, 1989a: 26).	
Quercus parvula var. shrevei	**Shreve's oak**
No contemporary uses identified to date.	
Rosa gymnocarpa	**Wood rose**
NW: Hips made into a tea taken for diabetes or when catching a cold. Juice of cut, fresh hips applied to insect bites (Ortiz and others 2006: 214). Juice used for healing sores (Colegrove 2006).	
Rhododendron spp.	**Rhododendron, including azaleas**
Blossoms used for household decoration (Colegrove 2006, Spinks 2006a).	
Sequoia sempervirens	**Coast redwood**
NW: Old-growth and second-growth boles used by Yurok individuals to make dugouts (miniature and full size) (Colegrove 2006, McCovey 2006, Ortiz 1990/91: 12-16).[17] Wood used to make framework of the square drums beaten while singing songs during the Indian card game (see Pacific yew for more about this game) (Ortiz 1993/94: 19, 2002: 4, 5). Wood carved into stakes to hold cuts of fish placed along the periphery of an oval-shaped roasting "pit" covered with hot coals. Not only is the wood soft and easy to carve, but the stakes hold water when soaked, insuring they will not burn and fall into the pit (Colegrove 2006, Ortiz 1998: 29).[18] Wood used to carve cooking paddles for stone boiling and figures for contemporary, culturally-inspired art (Ortiz 1991: 9, 10, 1995: 33).[19] C: Dolls made from shredded redwood bark by Kashaya Pomo (Ortiz 1989b: 13-14).[20] Shingles and shakes used in ceremonial house construction.[21]	
Trientalia latifolia	**Western starflower**
No contemporary uses identified to date.	

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[17] Field data 1990 to 2006.
[18] Field data 2006.
[19] Field data 1990.
[20] Field data 2005.
[21] Field data 1993 to 2006.

<table>
<tr><td><i>Umbellularia californica</i></td><td>Pepperwood
California bay laurel
Oregon myrtle</td></tr>
<tr><td colspan="2">NW: Fresh leaves placed in water and boiled to make aromatic steam to treat colds and sinus infections. Newly-grown, light-green tips used to treat toothache. Leaves poulticed on shingles. Mashed, fresh nutmeats poulticed on boils, blood poisoning, snake and spider bites and sores. Roasted nutmeats eaten for enjoyment, to prevent allergies in the spring, to prevent colds and flu in the fall, to relieve colitis and to relieve ulcers. Leaf oil used to treat earaches (Ortiz and others 2006: 68-69). Featherwork and baskets stored with leaves to repel insects. Leaves used for ceremonial purification (Colegrove 2006, McCovey 2006). Leaves placed in boiled water and steam breathed, while head covered with blanket, to relieve sinus infections (McCovey 2006). Branches fashioned into drumsticks (Ortiz 2002: 6). Wood used for net-making shuttles (Ortiz 1999/00a: 35, Spinks 2006). C: Roasted nuts eaten for enjoyment, sometimes pounded and shaped into balls and logs (Ortiz 1989a: 25, Smith 2004).[22] Fresh leaves used to make animal sounds (Ortiz 1992a). Branchlets used for ceremonial purification.[23]</td></tr>
<tr><td><i>Vaccinum ovatum</i></td><td>Evergreen huckleberry</td></tr>
<tr><td colspan="2">NW: A teaspoon of new, light green leaves dried and steeped in cup of boiled water for insomnia. One cup of tea taken two to three times a day by diabetics to relax. Berries eaten raw, canned and cooked in pies and “duff” (sweetened dough balls cooked in sweetened, thickened berries, spiced with cinnamon) (Ortiz and others 2006: 63, 64, 112, 148). Berries considered a staple by the Karuk and frozen for year-round use (Glaze 2003). C: Berries eaten (Ortiz 2000: 21).</td></tr>
<tr><td><i>Viburnum ellipticum</i></td><td>Western viburnum</td></tr>
<tr><td colspan="2">No contemporary uses identified to date.</td></tr>
<tr><td colspan="2">Associated Plant Species</td></tr>
<tr><td><i>Abies concolor</i></td><td>White fir</td></tr>
<tr><td colspan="2">NW: Pitch steeped in hot water for 15 to 20 minutes, then sticky substances strained off, to make gargle for sore throat (Ortiz and others 2006: 126). Wood used in brush dances (McCovey 2006).</td></tr>
<tr><td><i>Abies grandis</i></td><td>Grand fir</td></tr>
<tr><td colspan="2">NW: Pitch steeped in hot water for 15 to 20 minutes, then sticky substances strained off, to make gargle for sore throat (Ortiz and others 2006: 126). Used for Christmas trees (McCovey 2006).</td></tr>
<tr><td><i>Abies magnifica</i></td><td>Red fir</td></tr>
<tr><td colspan="2">NW: Pitch steeped in hot water for 15 to 20 minutes, then sticky substances strained off, to</td></tr>
</table>

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[22] Field data 1983 to 2006.

[23] Field data 1993 to 2004.

make gargle for sore throat. Insect-resistant wood may be used for holding featherwork (Ortiz and others 2006: 126).	
Acer circinatum	**Vine maple**
No contemporary uses identified to date.	
Arctostaphylos columbiana	**Hairy manzanita**
No contemporary uses identified to date. See *A. manzanita*.	
Calcycanthus accidentalis	**Spicebush**
C: Kashaya Pomo spiritual plant.[24]	
Ceanothus thyrsiflorus	**Blueblossom**
NW: No contemporary uses identified to date. Another species, *Ceanothus integerrimus*, lathered for soap; its pruned shoots used for warps in fine baskets (Ortiz 1998: 26, Ortiz and others 2006: 230).	
Clintonia andrewsiana	**Andrew's clintonia bead lily**
No contemporary uses identified to date.	
Corylus cornuta	**California hazelnut**
NW: Nuts eaten raw, dried like walnuts, or baked. Strong, straight, flexible shoots (from plants burned every two years in the fall) used as warp and weft in work baskets, such as eel traps, baby, "handle" and clothes baskets (Colegrove 2006, McCovey 2006, , 1996/97: 27-28, 29, 30, 1998: 24-25, Ortiz 1999: 17, Ortiz and others 2006: 15-16, 30, 68, 140). Eels pierced with hazel sticks and hung from them in smokehouses. Salmon strips tied with string looped over hazel sticks and hung from them in smokehouses (Ortiz 1999: 17, 18). Twisted hazel used as an element in fish dams and to fasten house poles together (Ortiz 1999/00: 33).	
Dryopteris arguta	**California wood fern**
No contemporary uses identified to date.	
Fraxinus latifolia	**Oregon ash**
No contemporary uses identified to date.	
Gaultheria shallon	**Salal**
NW: Berries eaten raw or canned (McCovey 2006, Ortiz and others 2006: 218). Used ceremonially (McCovey 2006). Berry used as a Jump Dance headpiece dye (Ortiz 1999/00: 32).	
Osmorhiza berteroi	**Sweet cicely**

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[24] Field data 1983 to 1993.

(=O. chilensis)	
NW: *Osmorhiza chilensis*, *O. occidentalis*, and *O. Purpurea* used to make childhood drink by steeping the above-ground plant in water (within living memory). According to Josephine Peters (Karuk), “We used to chew it, and play with it, and drink it all the time, because it had a good taste” (Ortiz and others 2006: 85)	
Rubus spectabilis	**Salmonberry**
NW: Berries eaten raw (McCovey 2006, Ortiz and others 2006: 219). Berries canned (McCovey 2006).	
Taxus brevifolia	**Pacific yew**
NW: This extremely durable wood used for hunting and ceremonial bows, spoons and eel hook handles (Colegrove 2006, McCovey 2006, Ortiz 1995: 31-33). Straight, knotless and limb-free branches gathered in fall when sap down, seasoned for a year, and fashioned into bows (Ortiz 1995: 32). Wood used for eel hook handles, some three feet long, with finger notches and designs (Gordon 1996/97: 9). Wood the primary material for the twenty or so sticks (“cards”) used by men when playing “Indian card game,” a gambling game in which teams earn points when their players correctly guess in which hand a member of the opposite team has hidden the “ace,” a yew stick marked with a black ring (Ortiz 2002: 4). Wood used for stick game “sticks” and “tossels” (two wooden blocks connected by a cord). During this very competitive and physically challenging game, on which wagers are placed, men compete to throw the tossel across their team’s goal line. Wood used as an element of ceremonial regalia (Colegrove 2006). Wood used by artisans for culturally-inspired carvings, such as “Yew Woman” by George Blake (Hupa/Yurok) (Ortiz 1995: 30, 33-34). Wood preferred for pipes, although madrone, oak, and manzanita can also be used (Ortiz 1993/94: 20).	
Torreya californica	**California nutmeg**
No contemporary uses identified to date.	
Toxicodendron diversiloba	**Poison oak**
NW: Leaflets eaten in small amounts to cause immunity to rash. Juice used for tattooing (Ortiz and others 2006: 206-207). C: Young, tender, partially-grown leaflets eaten in small amounts to prevent colds (Ortiz 1994b, 2002b: 157-160). Poison oak roots become intertwined with those of “Indian tea” (yerba buena), and by drinking the tea when young, one may develop an immunity to poison oak oils (Colegrove 2006).	
Vancouveria planipetala	**Redwood ivy**
No contemporary uses identified to date.	

California Indian Perspectives About, and Response to, Sudden Oak Death[25]

Many California Indians fear that SOD's spread may have irreversible effects on their ability to continue their cultures. A very real possibility exists, for instance, that tanoaks may be entirely eliminated from the landscape in infected areas. Even if the trees continue to exist somewhere else, traditionalist California Indians believe that when gathering cultural materials, it is both spiritually and ethically important to gather within their own tribal territory, in a place where no other family or individual has cultural rights to do so.

In the past, whenever California Indians went into another tribal territory to trade, or, more rarely, to gather, they showed respect for that tribe by doing so only with permission. Today, traditionalist California Indians continue to follow these older ways.

As explained in 2006 by Eric Wilder (Kashaya) about the importance of place to his people, "Part of the belief is that...our teachings to our people come from the land that we come from. The land recognizes our language, and considers us part of the landscape itself. So for us, to go outside of that to another place that recognizes a different group of people's language, we're not only disrespecting them, we're disrespecting the land."

The prayers, offerings, ceremonies, and cultural proscriptions that apply to the gathering of acorns, likewise apply to where, when and in what context traditionalist California Indians gather any plant materials. As Eric Wilder (2006) elaborated about Kashaya traditional law, "You have these rules to follow... As we gather, we use these places as classrooms for our children. We teach them that we're going out here to gather from the creation, and this is something we should respect. We're gathering something that we didn't plant here. The Creator planted these things here for us. We're taking it freely, but we need to sacrifice for it. We put up a picnic to respect the top of the land spirits; to thank the Creator for putting these things here for us."

When traditional law is not followed, acorns and other cultural plant materials "won't come back and won't be here for us the following year." Thus, for traditionalist Kashaya, the recent arrival of SOD into their tribal territory signifies a consequence for not respecting the rules: "The top of the land spirits and the plants and animals are rebelling against us, and trying to teach us that we're breaking the agreement that we had since we were first put on the land" (Wilder 2006).

In an effort to stem the advance of SOD into their ancestral territory, including their 41-acre rancheria, staff, and tribal members of the Kashaya Band of Pomo Indians have teamed up with researchers, such as Doug Schmidt of the Garbelotto Lab, and plant pathologist Ted Swiecki, to study whether Agrifos (phosphite, an inorganic salt), when applied to the surface of tanoak bark, can protect tanoak stands from *P. ramorum*. Since tanoak acorns continue to be used for food by the Kashaya, an important first step is to test whether phosphite will "affect the balance of tannins or otherwise affect acorn quality" (Spring 2006:19).

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[25] Unless otherwise indicated, all information about California Indian responses to this disease is derived from field research conducted from 2003 to present.

The Kashaya are one of several federally recognized tribes that have sponsored educational forums to alert their members about *P. ramorum*, and ways to prevent its spread, as have various tribal organizations. The Hoopa Valley Tribe, whose reservation does not currently have the disease, has instituted an active monitoring program using stream baiting with rhododendron leaves. Through this method, the tribe can monitor some 70 percent of their approximately 80,000-acre reservation in an effort to try and insure that the disease does not get established there. They are also working with the University of California, Davis, to sample for symptomatic trees. As a precaution, they have sponsored efforts such as bicycle-washing stations for mountain bike riders that come from afar to participate in races on the reservation (Salberg 2006).

California Indians openly wonder whether or not the discontinuance of ancestral land management practices honed over thousands of years has aided *P. ramorum*'s ability to spread. This lack of management has created unbroken thickets of understory. If woodlands and forests were once again more open, they argue, it would be more difficult for the disease to move from host to host. Other potential impacts might also be avoided. As explained by forester Kathy McCovey (2003),

"When you get an area too stocked with any type of species, the whole population gets weak. We've already got diseases hitting these trees. The tanoaks are dying. The maples and madrones, they're already stressed out. If we get SOD in there..., it will affect the majority of the species that we have along the river corridor. You'll have more dead trees. Then if you get a wildfire in there, it's going to burn hot. There's not going to be anything left but bare ground, because of the fuel loads and density of the trees. It's going to affect the soil."

Whether or not the return of indigenous land management practices will ultimately halt or reverse the spread of Sudden Oak Death, California Indians speak with assurance that the widespread reintroduction of these practices would be of overall benefit to the health of entire ecosystems.

In the meantime, California Indian plant gatherers worry that they might inadvertently spread SOD while continuing to practice their culture. As noted by Don Hankins (2003):

"We're more mobile today than we've ever been. We have this ability to go to the coast in these areas where SOD might be, and we might be hiking, or even collecting plant materials, and if we're not careful about what we do, we could potentially track this material back into our areas on our shoes, our gathering equipment, our tools, and so forth, and possibly introduce this into our own gathering sites."

Some individuals have stopped gathering anything at all in affected areas, even those who are aware of such safeguards as washing soil from shoes, boots and tires before leaving the gathering site, or cleaning shoes and boots with Lysol or a 10 percent bleach solution before leaving an infested site. They simply do not want to take the risk, especially since the disease is virtually impossible to identify in the field.

If affected areas encompass an individual's tribal territory, avoidance is not an option, given the cultural, emotional, spiritual, and historical ties that connect people to place.

Conclusion

For untold eons, California Indians have interacted with plants in ways that bridged physical and ecological needs with the intangibles of sacred time and cultural proscriptions. Their land management practices insured the health and well-being of the plants upon which they and other animal species relied. In the process of gathering plants, they developed a relationship with them.

Historical events altered those relationships, but did not sever them. Today, California Indians continue to use oak, tanoak, and many other plant species for the same purposes as their ancestors, creatively blending the older ways with newer techniques. The spread of SOD into several coastal and near-coastal, California counties threatens this vital relationship between people, cultural heritage, place, and plants. As California Indians grapple with the cultural and ecological implications of SOD, they face new challenges to the continuance of their cultures.

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Continue

A Resurvey of Oak Woodland Landowners: 1985, 1992, and 2004[1]

Lynn Huntsinger,[2] Martin Johnson,[2] Monica Stafford,[2] and Jeremy Fried[3]

Abstract

Results of a 1985 survey of California hardwood rangeland landowners were used to develop a multi-agency research and extension program, known as the Integrated Hardwood Range Management Program. In 1992 and in 2004, owners of the same properties were re-surveyed, regardless of whether or not the properties had changed ownership. Some highlights of the results are reported here. Although the survey cannot prove the program is the sole or direct agent of change, program-sponsored education and research aimed at encouraging oak rangeland owners to change oak management practices is reflected in changes in key landowner behaviors. Owners were less likely to value oaks for fuelwood, and less likely to cut oaks down. In addition, there was a significant increase in landowners planting oaks. Consultation with Cooperative Extension advisors and specialists about oaks continued to increase. Other changes also reflect the changing times: landowners reported that land trusts were as often consulted about oaks as Cooperative Extension advisors and specialists. About 6.5 percent of them had a conservation easement on their property, and the number of oak woodland landowners engaged in production of crops or livestock continues to decline. On the other hand, the number of landowners, including ranchers, who say they live in the oak woodland to be near natural beauty, for recreation, and to have a different lifestyle, is increasing.

Keywords: Easements, extension, grazing, land use, management, values.

Introduction

A 1985 statewide survey of the goals, characteristics, and management practices of California hardwood rangeland landowners was instrumental in developing the research and extension components of the multi-agency "Integrated Hardwood Range Management Program" (IHRMP) (Huntsinger and Fortmann 1990; Huntsinger and others 1997). As coordinated among the University of California Cooperative Extension, the California Department of Forestry and Fire Protection, the California Department of Fish and Game, and other agencies, program goals at the outset included reducing the loss of oaks in the state and researching ways to encourage appropriate management of the woodlands by landowners. The vast majority of California's hardwood rangelands are privately owned. In order to develop effective research programs and education materials, it was necessary to discern who the owners of hardwood rangelands were, what their goals were, and to what kinds of outreach approaches they would be most receptive. In 1992, and again in 2004, the owners of the same random selection of properties from 1985 were re-surveyed,

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[2] Professor and Graduate Student Researchers, Environmental Science, Policy, and Management, University of California, Berkeley, 94720.

[3] Research Forester, Forest Inventory and Analysis Program, USDA Forest Service Pacific Northwest Research Station, Portland, OR.

regardless of changes in ownership or land use. This paper highlights some results of a comparison of the results of the third survey to those of the first, comparing responses in 1985 to those in 2004.

Previous surveys identified groups of landowners with quite different interests and characteristics, indicated that ownership of the woodlands was fairly fluid, and showed fragmenting of parcels by subdivision to be a growing problem in the woodlands (Fortmann and Huntsinger 1989, Huntsinger and others 1997; Huntsinger and Fortmann 1990). In the first survey, owners of large and small properties were compared, and two hardwood rangeland landowner archetypes were described, each owning at least a third of the woodlands (*table 1*) (Huntsinger and Fortmann 1990). These archetypes were used to develop education packages targeted to landowners statewide. Re-surveys allow a rare opportunity to examine trends in land ownership, land uses, and management practices since 1985, and to obtain insight into the effectiveness of the IHRMP. The objectives of the 2004 survey were to:

1. Contribute to the further development of the Integrated Hardwood Range Management Program's education and research activities, and provide information for legislators.
2. Examine changes in demographic characteristics, attitudes, management practices, land use, and use of outreach services, of hardwood rangeland landowners in 2004 in order to update the IHRMP clientele profile.

Here we present selected results of relevance to the development of IHRMP programs.

Table 1—*The hardwood rangeland archetypes identified as characterizing respondents in the 1985 and 1992 surveys.*

Owner of Small Property	Owner of Large Property
doesn't sell products from land	sells products, most often livestock
more often absentee	resident owner
more recent arrival	long term owner
relatively amenable to oak use regulation	anti-regulation
less than half cut living oaks	most cut living oaks
growing in numbers	relatively stable in numbers

Methods

To allow comparison, the 2004 survey was designed to have many questions in common with the previous survey, though questions about conservation easements and land trusts were added because of their high visibility in oak woodland conservation. Surveys were pre-tested with selected landowners not part of the study sample, and then private owners of hardwood rangeland throughout the state were surveyed by mail, using the standard four-wave technique described by Dillman (1978) to achieve a high response rate. The greater the response rate, the less “self-selection” bias influences responses and hence the more representative the sample.

Questionnaires were sent to the owners of land containing the Forest Inventory Assessment plots previously used to assess hardwood volume in California (Bolsinger 1988). The plots were established at the intersection points of a randomly established 11-square-kilometer grid overlaid on the state. Plots designated as "Hardwood Woodland Type," (U.S. Department of Agriculture, Forest Service 1981) were selected for this study if there was an overstory of 10 percent or greater canopy cover of *Quercus spp*., and the plot was on private land. By definition, these lands do not show evidence of ever having had 10 percent or more cover of trees of industrial roundwood species. Plots with these characteristics occurred in 38 of the state's 58 counties, at elevations ranging from 80 to 1,800 m.

Questionnaires were returned by 126 of 166 eligible respondents for a response rate of 76 percent in 1985, 121 of 151 eligible respondents for a response rate of 80 percent in 1992, and 98 of 185 eligible respondents in 2004-2005 for a response rate of 69 percent. These are, the "n" values, with some slight variations, for each year. We believe that our declining sample size is due to the fragmentation of the woodlands, as well as transfer of ownerships that we were unable to track. When properties were divided up and sold, we were not able to discern which of many new smaller properties held the plot. About 30 percent of non-respondents were corporate, compared to 21 percent of respondents, and 11 percent of non-respondents were trusts, compared to 8 percent of respondents. Despite losses from the sample, due to the subdivision of properties that made locating new owners often impossible, 272,624 ha were owned by our respondents, more than 10 percent of California's total hardwood rangelands (CDF-FRRAP 2003). In 2004, every effort was made to locate and survey new owners of properties in the sample. The 2004 respondents include those who purchased, inherited, or took over management of a family property since 1985, and some who did not respond to previous surveys, as well as those maintaining ownership of the property since 1985. Of the 48 non-respondents in 2004, eight were limited holding companies or corporations, four were trusts, and two were land investment companies.

The grid method used to establish Forest Inventory Plots means that larger properties have a greater probability of being selected for the sample (Wensel 1983). While this resulted in a sample with good representation of landowners of each property size, it means that responses about land use practices cannot be directly extrapolated to the hardwood rangeland as a whole. Analysis weighting the sample inversely to the size of property can be used to extrapolate findings to a statewide spatial proportion of the hardwood rangelands meeting our selection criteria (Huntsinger and others 1997). Another consideration is that while a landowner may report that they "cut oaks," we do not know how many hectares or oaks the landowner cut. What we do know is that a landowner of a certain number of hectares engages in the practice of cutting oaks. The sampling frame and methodology were consistent for all three surveys, facilitating evaluation of changes in landowner characteristics, values, and practices over time. The Chi-square statistic was used to determine significance for categorical variables, with all results of $p < 0.10$ reported as significant, while a t-test was used to compare grouped continuous variables, again using $p < 0.10$ as the cutoff for significance (Spicer 1972). Unless otherwise stated, statistical comparisons are between the 1985 and 2004 samples.

Landowners were asked about their demographic characteristics, attitudes, land tenure, land use, and management practices. Questions are condensed in the tables presenting results. Here we highlight results of most relevance to the IHRMP.

Results

Overall, landowners still fall into the archetypes described as a result of the 1985 study (Huntsinger and Fortmann 1990; *table 1*). Relationships between property size and landowner goals, attitudes, and practices remain consistent with those of the results of the 1985 survey (Huntsinger and Fortmann 1990). There has been no significant change in landowner demographic characteristics, such as residence on property, age, education, income, absentee ownership, or length of ownership since 1985. Owner age averages late 50s to early 60s. More than half are college graduates, more than half have had the land in the family for more than 20 years, and less than a quarter are absentee owners. However, since 1985 changes have been made in land status, owner characteristics, management, and attitudes about oaks.

Declining Livestock Production

Significant changes have occurred in sources of income and production activities since 1985 (*fig. 1*). Significantly fewer owners are earning their income from ranching or farming ($p < 0.08$).

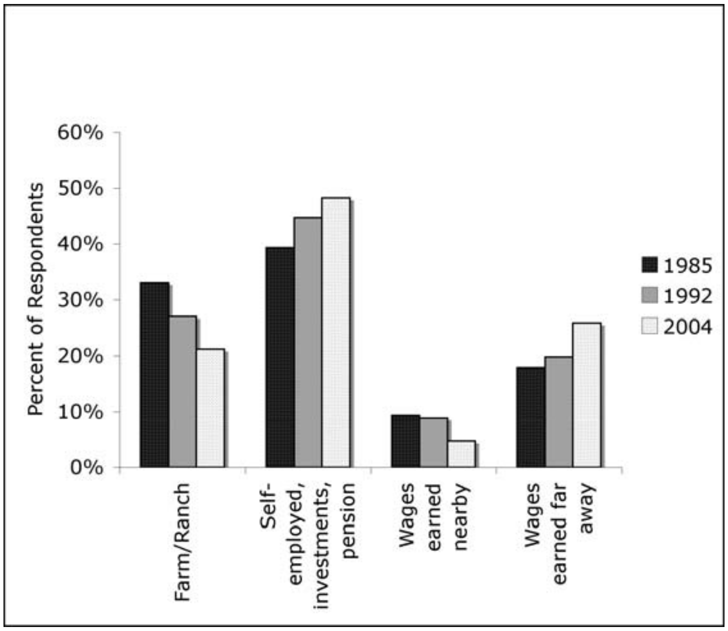

Figure 1—Respondent major source of income, 1985, 1992, and 2004.

Since 1985, the proportion of owners reporting livestock grazing on their property has declined from 73 percent to 62 percent ($p < 0.08$), though this decline has apparently leveled off since 1992. The proportion of landowners reporting that they sell livestock has dropped from 61 percent in 1985, to 55 percent in 1992, and finally to 41 percent in 2004 ($p < 0.00$). A similar decline took place in reported membership in livestock associations or the farm bureau, from 58 to 41 percent since 1985 ($p < 0.06$).

Using the weighted sample, about 42 percent of oak woodlands are owned by those who raise livestock for sale, while another 10 percent of the woodlands are owned by those who produce livestock for their own and guest use only. The remaining 10 percent of the grazed woodlands are owned by landowners that lease out their land to ranchers. The mean property size of those with grazing on their properties has increased from 30 ha in 1985 to 67 ha in 2004 ($p < 0.03$, t-test). Looking at the larger properties alone, more than 80 percent of woodland parcels larger than 80 ha are grazed by livestock, a proportion that has not significantly changed since 1985. Interestingly, the proportion of landowners using their land for hunting and fishing has also declined significantly ($p < 0.02$) from 1985 to 2004 – from 66 percent to 48 percent, respectively.

Oak Woodland Ranchers

Because they own so many of the larger properties, livestock producers are of special interest to those concerned with landscape-scale conservation. After isolating livestock producers from the rest of the sample, only about one-fourth of oak woodland ranchers reported that the majority of household income came from ranching, down from 40 percent in 1985 ($p < 0.04$), while 10 percent reported farming as their major source of income. About 22 percent cited off-ranch wages as their major income source, and another 38 percent earned most of their income from other forms of self-employment, including investments, pensions, and so forth.

The vast majority of ranchers produce cattle only. Less than one-fifth of oak woodland landowners grazed goats, sheep, or llamas, and most of those also grazed cattle. Most stockers were reported by ranchers that also have a cow-calf herd, with less than one-tenth of oak woodland cattle producers raising stockers alone in 2004.

The motives ranchers gave for choosing to live in the oak woodland changed dramatically and significantly from those given in 1985, with recreation, natural beauty, getting away from the city, and having a different lifestyle becoming significantly more important to ranchers as reasons to live in the oak woodlands (*fig. 2*; $p < 0.06$). The number saying that a family business or property influenced their choice did not change significantly. Though only asked about in the most recent survey, 59 percent of ranchers stated that hunting and fishing influenced them, and 82 percent said that opportunities to view wildlife influenced their decision to live in the oak woodlands. These patterns are common among non-ranching oak woodland owners as well.

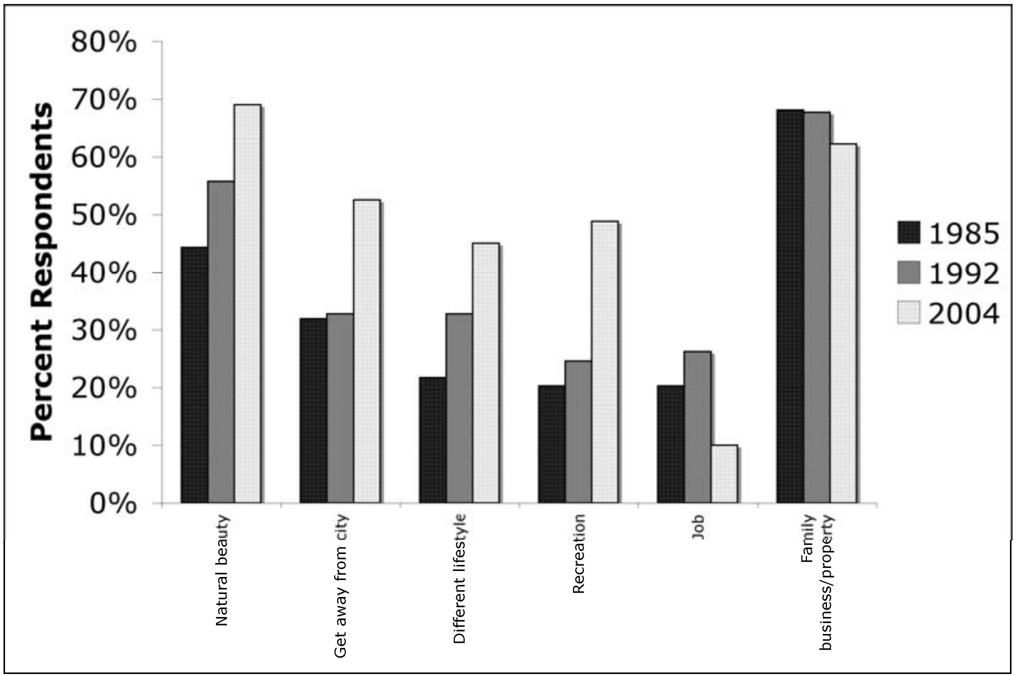

Figure 2—Factors that strongly influenced the oak woodland rancher's choice to live in the oak woodlands, 1985, 1992, 2004 (N=173).

Oak Management

The majority of landowners have reported valuing oaks for property values, shade, erosion control, wildlife habitat, natural beauty, and browse throughout the years of the survey. There has been a significant increase in the number of landowners stating that they value oaks for conserving water, from 46 to 62 percent ($p < 0.05$), and a decline in the number who value oaks for fuelwood – from 63 to 37 percent ($p < 0.00$). Changes in values are apparently reflected in changes in behavior. There has been a strong and significant reduction in cutting living oaks for any purpose – from 83 to 61 percent ($p < 0.00$) – while the proportion of landowners reporting that they thin oaks has remained unchanged at about a third. The number of owners engaged in the sale of firewood, whether standing or down, declined by half, to 9 percent ($p < 0.03$), and those cutting oaks for home firewood has declined from 41 to 16 percent ($p < 0.00$). The percentage of landowners cutting oaks to increase forage production, 24 percent, remains significantly lower than in 1985 when it was 39 percent ($p < 0.01$), but has not changed since 1992.

About one-fourth of owners in 2004 reported an inadequate number new oaks coming up to replace the old oaks – 56 percent said there were enough new oaks, and 18 percent reported that they did not know. This question was not asked in previous surveys. The landowner's perception of the abundance and reproduction of oaks is related to whether or not they cut oaks. Landowners who believe there is adequate oak replacement, or have oak canopy cover greater than 50 percent on their property are significantly more likely to cut oaks ($p < 0.01$; *table* 2). Those who have less than 50 percent canopy cover believe oaks are being lost and agree oak harvest should be regulated, are less likely to cut oaks ($p < 0.01$; *table 2*). Cutting oaks to increase forage is also significantly related to perceptions of oak replacement and the belief that oak use should be regulated ($p < 0.01$; *table 2*).

Table 2—*Oak cutting and perceptions of woodland condition, 2004*.

If the landowner…	Then, % landowners that have cut one or some oaks for *any reason*	Then, % landowners that have cut one or some oaks to *increase forage*
Believes there is adequate oak replacement	86%	36%
Believes there is inadequate oak replacement	48%	13%
Has oak canopy > 50%	94%	38% (ns)
Has oak canopy < 50%	57%	22% (ns)
Agrees that oaks are being lost in California	53%	17% (ns)
Agrees oaks should be regulated	39%	7%
EXPECTED (% total sample)	65%	24%

A dramatic and significant change has been made in how landowners manage oaks. The number of landowners planting oaks has increased dramatically ($p < 0.00$; *fig. 3*), while the number spraying, girdling, or poisoning oaks has declined to almost none ($p < 0.01$). More than one-third of oak woodland landowners state that they carry out practices to improve wildlife habitat.

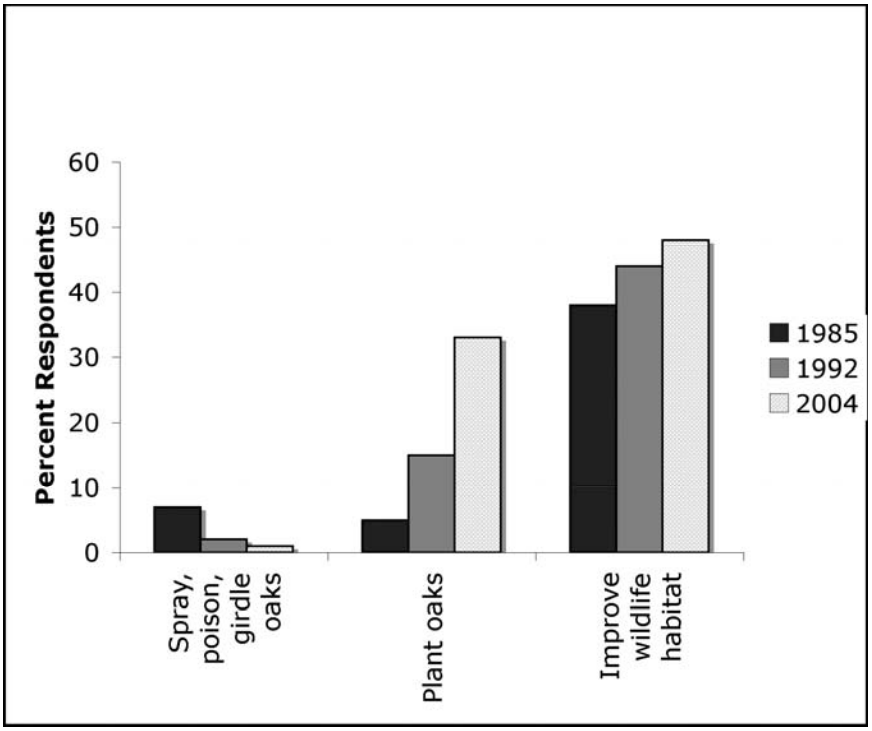

Figure 3—Respondent carried out the following practices in the last five years, 1985, 1992, and 2004 (N = 345).

Using a scale developed by summing the frequency of carrying out four oak-promoting management practices, we can compare the behavior of those who value oaks for certain purposes to those who do not. The three practices are planting oaks, maintaining a fixed oak stocking level, and cutting mistletoe out of trees. Landowners who value oaks for shade ($p < 0.01$, t-test), wildlife habitat ($p < 0.01$, t-test), wildlife and livestock browse ($p < 0.04$, t-test), and beauty ($p < 0.00$, t-test) are significantly more likely to carry out oak-promoting activities. Valuing oaks for soil protection, shade, forage, fuelwood, property values, or water conservation did not show this relationship.

Advice: Extension and Land Trusts

Also using the scale of oak-promoting practices, landowners receiving advice about oaks from University of California Cooperative Extension advisors or specialists within the last two years ($p < 0.03$, t-test), and in fact from any public advisory service, were significantly more likely to carry out oak promoting practices ($p < 0.00$, t-test).

Consultation with advisory agencies increased overall, with significantly more landowners consulting about oaks with the Natural Resource Conservation Service and University of California Cooperative Extension specialists and advisors at each survey point (*table 3*). Though not asked about on the previous two surveys, 17 percent of landowners reported getting advice from or discussing oaks with a land trust.

Table 3—*Chi-square test results (df = 2) for landowner consultation with advisory services in last two years, 1985-2004.*

Landowner consulted with the following in last 2 years:	% landowners			P-value
	1985	1992	2004	
Cooperative Extension	4	13	16	.00
Natural Resources Conservation Service	6	6	15	.02
California Dept. of Fish and Game	7	7	12	ns
U.S. Forest Service	5	4	5	ns
California Department of Forestry	11	8	8	ns
Any public advisory service	19	21	25	ns
Private oak expert	10	12	7	ns
Book	--	--	23	--
Land Trust	--	--	17	--

The number of land trusts in California has been increasing rapidly in recent years (Land Trust Alliance 2005). In a 2001 three-county survey of ranchers (Liffmann and others 2000) 4 percent reported having a conservation easement on their property. In this survey, 6 percent said they had a conservation easement on their property, while 10 percent reported that they did not know whether they did or not. Considering the entire sample of landowners, 30 percent had an easement or would consider one, 43 percent are not interested in a conservation easement, and 26 percent don't know about them or enough about them. When asked if they had ever been approached about selling or donating an easement, 26 percent said yes.

Though only asked about in 2004, two-thirds of landowners reported that they planned to keep their land intact for the next 10 years, while 11 percent reported that they planned to sell or give away all or part of their property within the next 10 years. The proportion with land in the Williamson Act has remained steady at slightly more than half. Significantly more hardwood rangeland landowners reported living “less than 5 miles from a subdivision” ($p < 0.09$), from 52 percent in 1985 to 61 percent in 2004.

Attitudes About Regulation

At least three-fourths of all landowners have agreed on each survey that regulation leads to a loss of liberties and freedom. At the same time, more than 80 percent of landowners agreed each time that protection of water quality should be a state responsibility, and more than three-quarters have agreed that oaks are being lost since 1992—significantly more than in 1985 ($p < 0.02$). The number agreeing with the statement that "citizens should be able to use natural resources on their own land without asking state permission" has decreased significantly at each survey point ($p < 0.00$), from 90 to 72 percent between 1985 and 2004. Nonetheless, the number agreeing that oak use should be regulated has not increased significantly, ranging from 32 percent in 1985 to 43 percent in 2004.

Discussion

Since 1985, significant changes have occurred in the goals and practices of those who own hardwood rangeland. Although this type of survey cannot "prove" that the IHRMP caused people to act differently, changes in values and behavior reflect program goals. Fewer landowners are cutting oaks and fewer value oaks for fuelwood or sell fuelwood. More owners are planting oaks, and more landowners, ranchers and others, believe that an important reason to live in the woodlands is for their beauty. Valuing oaks for beauty is linked to protecting and promoting them. Only one respondent reported spraying, girdling, or poisoning oaks. Overall, there seems to have been a real shift to caring for oaks. On the other hand, there is no consensus that oak use should be regulated. Landowners remain unfavorably inclined toward regulation, while recognizing that there is a valid state role in some aspects of natural resource management.

A landowner's beliefs about the status of oak woodlands, as well as the number of oaks on the property, influence behavior. Landowners with an oak canopy cover greater than 50 percent, and landowners who believe there is adequate oak replacement, are more likely to have cut down one or more oaks. Research has shown that an oak canopy of 50 percent or less does not reduce forge production, and in some cases, can extend the availability of green feed by increasing the species and phonological diversity of the grassland (Frost and McDougald 1989; McClaran and Bartolome 1989). A smaller proportion of those who agree that oak use should be regulated cut oaks.

An increasing number of oak woodland landowners are getting advice from Cooperative Extension advisors and specialists, and from NRCS, and this is apparently linked to practices that favor oaks. An important trend is that land trusts also are now commonly acting as sources of advice, an indication that it is valuable for extension and IHRMP to work with land trust managers and scientists. As most oak woodlands are privately held, it makes sense that advisory services oriented to private lands are most often consulted.

The majority of owners have livestock grazing on their property, especially in the larger ownership categories, but fewer of them are selling livestock themselves. The proportion of land used for grazing has not changed since 1992, a possible indication of an increase in leasing of private lands by the remaining producers. In a 2002 survey in the fast-growing central Sierra, foothill ranchers reported that leasing was an important source of forage for them, and many used multiple leases, public and private, to get through the year (Sulak and Huntsinger, 2002).

A landowner may choose to lease land for grazing for income, fire hazard reduction, and weed control, among other reasons. Working with land trusts, private owners, and homeowner's associations interested in leasing land for grazing might be considered for emphasis by IHRMP, to protect hardwood resources and to help encourage sustainable ranching. Striving to reach “non-production” landowners will continue to be an important part of oak woodland outreach; however, encouraging woodland conservation on the larger parcels still means reaching those producing and grazing livestock. Recent research has linked ranch sustainability in high-growth regions of the state to forage and pasture availability, including availability of leased public and private lands (Sulak and Huntsinger 2002). Exploring this relationship further will be important to conservation of working oak woodlands.

Conclusions

Twenty years ago, the IHRMP took on the challenge of conserving hardwood rangelands in California through education and research. The fact that most hardwood rangelands are privately owned was a particular challenge to conservationists, natural resource academics, and environmentalists long focused on public lands. A research and extension program initially centered on the technical aspects of how to improve grazing, wildlife, and oak management expanded to include planning and policy projects. At the same time, things were happening outside the program. Non-profit conservation organizations, notably land trusts, have become increasingly prominent participants in private land conservation. The development and growth of conservation easement programs, and in many cases, a decades-long process of mutual education has improved communication between groups like the Nature Conservancy and diverse types of private landowners. Landowner groups have successfully sought and created land trusts that reflected their own ideas about private lands conservation, such as the California Rangeland Trust. Public funds have been allocated to these groups for the creation of conservation easements. The Natural Resource Conservation Service and the Department of Fish and Game have invested in oak conservation through use of various incentive and advisory programs. The Natural Resource Conservation Service in particular has emphasized collaborative programs, and has been well-received in many areas.

Are all these efforts a substitute for regulation? Have oak woodlands been adequately conserved? These are questions that deserve more investigation. There is good evidence, some presented here, that landowners are being more careful of their oaks, and in fact many report planting them. Urban sprawl continues to fragment and destroy oak woodlands, but has the rate slowed, or have development patterns been influenced by the program in positive ways? Though conservation easements preclude conversion on easement lands, funding for easements is limited, and without some sort of coordinated effort protection of large contiguous areas is difficult to plan. If clean air, wildlife habitat, watershed, carbon sequestration, viewshed, and other values from oak woodlands could be better quantified, as “ecosystems services,” it would no doubt make more clear what is lost when land is paved and converted and improve public decision making. But a “market” for these services that would result in actual landowner compensation is less clear, though conservation easements do represent one such existing “market.” It is apparent that landowner values and public values for oak woodlands are in many ways convergent and converging. Protection of natural beauty and wildlife is valued by both landowner and the public. There is great opportunity to work with landowners to assure continued production of amenity values for public and private consumption, if values can be captured to help landowners keep their assets in extensive agriculture.

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Continue

Long-Term Growth of Coast Live Oak in Three California Counties—17-Year Results[1]

Lawrence E. Bonner,[2] Norman H. Pillsbury,[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 in 1984. Information about diameter, number of stems per acre, 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, 1996, and 2001.

Both basal area and total volume growth percentages were significantly greater in the thinned plots compared to the control plots. Average basal area per acre growth rates were 22 percent for the treatment plots and one percent for control plots. In general, total volume growth rates were nearly three times as great in the treatment plots compared to the growth plots. Mortality in unmanaged stands can substantially reduce the growth potential. Proper care and management of the woodland forest can reduce losses from fire and, in general, protect the value of the resource.

Keywords: Basal area, coast live oak, management, thinning, volume growth rate.

Introduction

Thinnings are normally conducted to stimulate the growth of the trees that remain and to increase the merchantable net yield of 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). A potential secondary benefit of thinning is to reduce mortality caused by accidental fire, since fire intensity may be lower in thinned versus unthinned stands.

Currently, little is known about site productivity, regeneration, tree growth, and the potential effects of harvesting, including intermediate thinnings, on coast live oak woodlands. The goal of this study was 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. Previously published papers described the methodology and rationale for the thinning regime and provide preliminary findings about the effects of thinning on coast live oak stands (Pillsbury and others 1987; Pillsbury and Joseph 1990; Pillsbury and others 1998). This paper extends our knowledge about the effects of thinning in coast live oak stands to a 17-year period.

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[2] Partner, Piedra Environmental Consultants, 155 Twin Creeks Way, San Luis Obispo, CA 93401. e-mail: larry_bonner@dot.ca.gov.

[3] Professors of Forestry, Natural Resources Management Department, Cal Poly State University, San Luis Obispo, CA 93407. e-mail: npillsbu@calpoly.edu and rpthomps@calpoly.edu, respectively.

The findings of this study should prove useful to foresters and land managers concerned with the management of coast live oak woodlands. It also will be helpful to landowners seeking information on strategies for managing their coast live oak woodlands.

Methods

Site and Plot Selection

Initially, 10 sites were selected for this study in Monterey, San Luis Obispo, and Santa Clara counties (*fig. 1, table 1*). Three plots were established at each site, consisting of one control plot (no thinning) and two plots that were thinned to 50-square-feet per acre (heavily thinned plots) and 100-square-feet per acre (lightly thinned plots), respectively. Plots were established in stands ranging in age from 40 to 85 years old.

Figure 1—Map of coast live oak thinning plots.

A change in ownership at one site required it to be dropped from the analysis in this paper. The analyses for all previous years were redone so that comparisons could be made for this paper. However, results presented in previous papers, based on all 10 sites, should not be compared to the results presented here in this paper.

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 and monumented for re-measure.

Table 1—*Location and treatment (control, lightly thinned, or heaving thinned), of study plots.*

	Treatment by site and plot number[1]		
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/Gonazales/Monterey	5-2	5-3	5-1
Rana Creek Ranch/Rana Creek/Monterey	7-3	7-1	7-2
Pesenti Winery/Templeton/San Luis Obispo	8-3	8-1	8-2
Prefumo Canyon/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] Site and plot, for example, 1-2 means Site 1, Plot 2.

Data Collection

The following information was obtained for each tree at least 1 inch in diameter at breast height in each plot in 1984, 1989, 1997, and 2001: tree number, species, diameter at breast height (inches), total height (feet), tree vigor code, and crown class. Additional tree information obtained during the initial inventory in 1984 included a 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.

Plot level information included: 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 plot information obtained during the initial inventory in 1984 included slope (percent), aspect, elevation, soil type, stand age, and site index. Plots locations were identified on USGS 7.5 minute topographic maps and on aerial photographs.

Development of Stand, Basal Area and Stock Tables

Standard mensurative data were compiled for each plot before and after thinning and extrapolated to a per-acre basis. Tree volumes for all hardwoods growing in the plots were expressed as total volume, wood volume, and sawlog volume. Total volume is the total outside bark volume including the stump. Wood volume is defined as the 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 diameter at breast height (dbh) and 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.

Results

Coast live oak plot data were analyzed for changes in stand density, growth volume, and mortality 17 years following the application of thinning treatments. The effects of thinning after 17 years on stand characteristics, including number of stems, basal area, and total volume, are discussed below. Analysis and results for wood volume, sawlog volume, tree movement by diameter class, analysis of understory data, clump analysis, sprout analysis, natural regeneration, the forage layer in the thinned plots, and woody shrubs can be found in Pillsbury and others (2004).

Number of Stems per Acre

Ingrowth

Changes in the number of stems per acre over the 17-year period would be due to either ingrowth or mortality. Trees were counted as ingrowth and included in the sample when they were at least 1 inch in diameter at breast height (4.5 ft). The first ingrowth was observed in the 1996 inventory with six trees, among the nine sites, being counted as ingrowth. Most changes in the number of stems per acre during the first 12 years were the result of mortality.

Ingrowth increased over time in the treated plots (*fig.* 2). The heavily thinned plots (50 ft^2 per acre) averaged 24.4 trees per acre ingrowth, while the lightly thinned plots (100 ft^2 per acre) averaged 11.1 trees per acre, and the control plots only 1.7 trees per acre. The largest amount of ingrowth was seen in Site 2. The heavily thinned plot had approximately 220 trees per acre of coast live oak ingrowth. The lightly thinned plot had 50 trees per acre of coast live oak ingrowth, and the control plot had no ingrowth. Seventeen years after t hinning, three sites had ingrowth, including Sites 1, 2, and 4. Within these sites, ingrowth occurred in one heavily thinned plot, two lightly thinned plots, and two control plots.

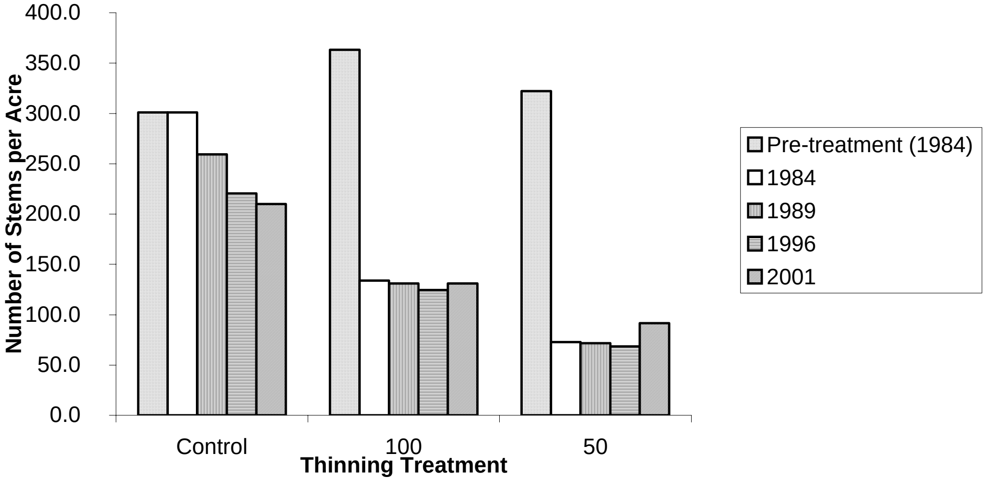

Figure 2—Number of stems per acre by treatment type. Treatments include control, lightly thinned (100), and heavily thinned (50) plots.

After 17 years, ingrowth was found in only three of the nine sites. Based on the analysis of clumps and sprouts found by Pillsbury and others (2004), the rate of ingrowth could be accelerated if some method of stump protection from browsing such as screens or piling brush on the stump was provided. Stump protection was not included as a part of this study.

Mortality

Mortality was most evident in the control plots (*fig*. 3). Wildfires that occurred during the summers of 1985 and 1994 were responsible for the majority of tree death that occurred. Three of the nine sites were affected by fire between 1984 and 1989 and one burned again between 1989 and 1996. An average of 81 trees per acre in the control plots was lost during the 12-year interval, and this impact was still evident in the 17-year analysis. Site 1 burned twice during this period with the control plot losing 325 of its 400 trees per acre due to fire. This plot represented 45 percent of the total mortality in all control plots. The control plot in Site 3 lost 235 of its 610 trees per acre due to snow damage and fire. The greater density of trees in the unthinned control plots certainly contributed to stand altering fire intensity and subsequent loss.

No fires occurred in the nine sites between the 1996 and 2001 inventories. The number of stems per acre in the control plots continued to decline slightly but at a much lower rate than measured in previous inventories. In total, an average of 92.8 trees per acre was lost in the control plots over the 17-year period. Eighty-seven percent of these trees were lost in the first 12 years due primarily to fire. The current mortality rate, based on the 2001 measurement year, still exceeds ingrowth in the control plots.

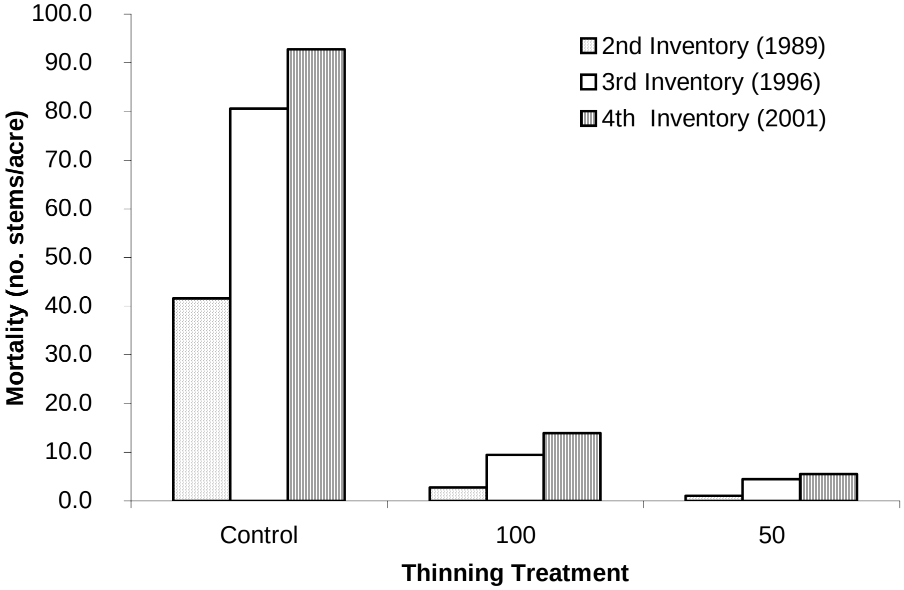

Figure 3—Mortality for control and treatment plots.

For the lightly thinned plots, mortality also exceeded ingrowth. Three of the lightly-thinned plots were burned at the same three sites yet a total of only 13.9 trees per acre were lost over the 17-year period, with an average of 9.4 trees per acre lost in the first 12 years. When an ingrowth rate of 11.1 trees per acre between the 1996 and 2001 measurement periods is factored into this picture, the number of stems per acre is now within 2.8 trees of the original number after thinning.

Unlike the control and lightly thinned plots, ingrowth now exceeds mortality in the heavily thinned plots. Even with fire burning three of the heavily thinned plots at the same sites as the control and lightly thinned plots, a total of only 5.6 trees per acre was lost over the 17-year period. With an ingrowth rate of 24.4 trees per acre between the 1996 and 2001 measurement periods, the result was an increase of approximately 18.9 trees per acre above the amount after thinning. Seventeen years after thinning, the heavily thinned plots had begun to show an increase in the number of trees per acre (*fig. 2*).

Basal Area per Acre

The thinning treatments were designed on the basis of reducing basal area. Changes that occurred between 1984 and 2001 are shown in figure 4.

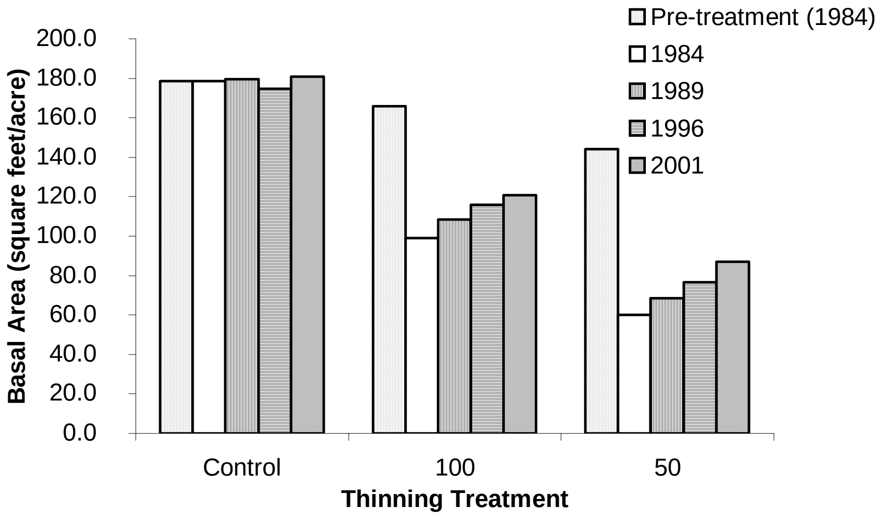

Figure 4—Basal area per acre for control and thinned plots.

The 17-year average increase for all control plots is 2.5 ft^2 per acre, or about 1.4 percent. For the lightly thinned plots, the increase is about 21.6 ft^2 per acre (22 percent) while the heavily thinned plots increased by about 26.8 ft^2 per acre (45 percent) over the same time period.

Throughout the 17-year period, the heavily thinned plots have continually increased in growth rate (ft^2 per acre, per year) and have now surpassed the lightly thinned plots in basal area production. This may be an indication that the trees in the lightly thinned plots are beginning to more fully occupy the site, and as a result, their growth rates are beginning to slow. The trees in the heavily thinned plots continue to benefit from an increase in the amounts of water, soil nutrients, and sunlight available after thinning.

Further, at the stand level, these data show that the heavily thinned plots averaged 11 times the basal area growth when compared to the control plots (*fig. 5*), and the lightly thinned plots averaged nine times the growth, compared to the control plots.

Because of the high rate of mortality in the control plots, it could be argued that these ratios and data might be somewhat misleading. But, one of the reasons for thinning a stand is to reduce the density quickly, speeding up the rate of natural mortality or mimicking a catastrophic event (fire), and to improve the vigor and growth rates of the residual stand. Dense stands will typically have higher rates of natural mortality in addition to higher death rates during catastrophic events, such as wildfire or extreme snowstorms. In an effort to provide a comparison of how surviving trees responded relative to control plots, the analysis of total volume was conducted only on living trees.

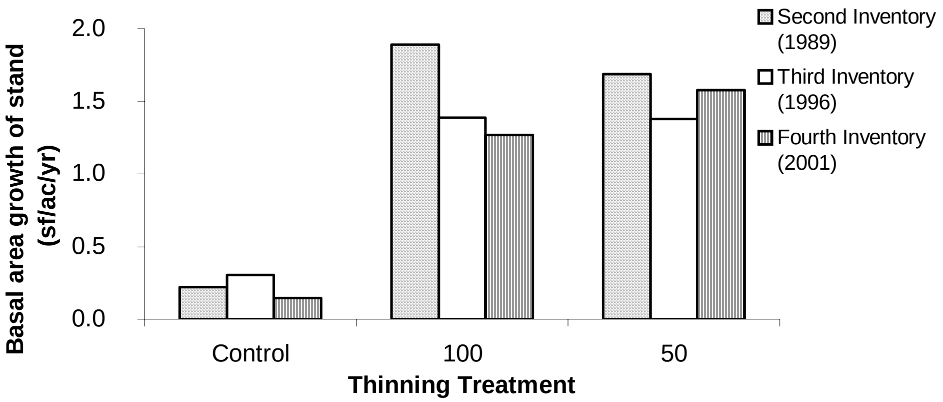

Figure 5—Basal area growth of stand for control and thinned plots.

Due to 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 17-year period, total volume increased by 984 ft^3 per acre (19.4 percent) for control plots (*fig. 6*). Total volume in thinned plots increased by 1,107 ft^3 per acre (38.1 percent) for the lightly thinned plots and by 1,174 ft^3 per acre (64.2 percent) for the heavily thinned plots.

As with basal area, the heavily thinned plots were beginning to out-produce both the control and lightly thinned plots in total volume growth after 17 years. After 12 years, the heavily thinned plots were the least productive and both the control and lightly thinned plots out-produced the heavily thinned plots (Pillsbury and others 2002). The shift in total volume production shows the ability of the heavily thinned plots to gain significant volume as a benefit from thinning. Even though the heavily thinned plots have fewer trees than the other plots, the growth is now being dispersed among these fewer but larger trees, resulting in an increase in growth and merchantable volume in the heavily thinned plots.

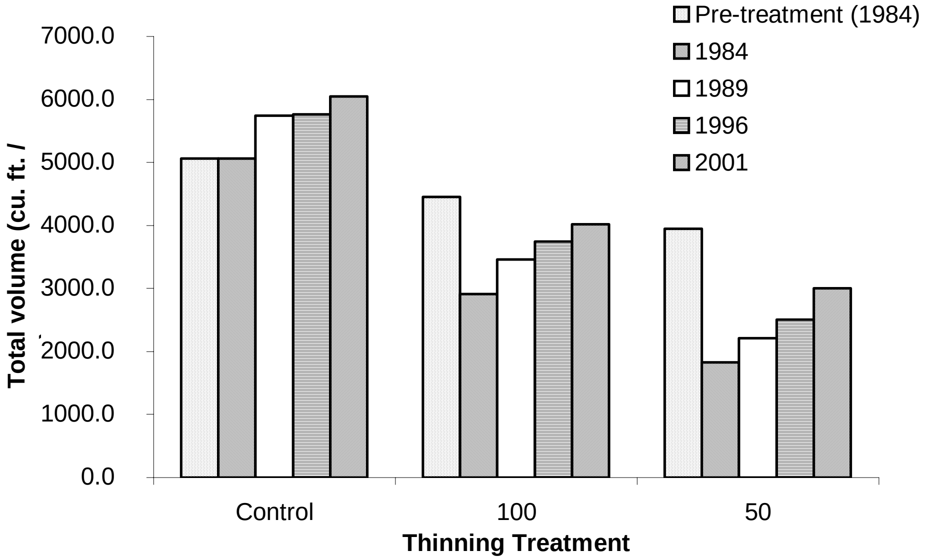

Figure 6—Total volume for control and treatment plots.

Volume growth per tree was greater in thinned plots than in control plots by substantial margins (*fig. 7*). Trees in the lightly thinned plots increased in volume by 56 percent compared to trees in the control plots, on average. Trees in the heavily thinned plots increased in volume by 147 percent more than trees in the control plots.

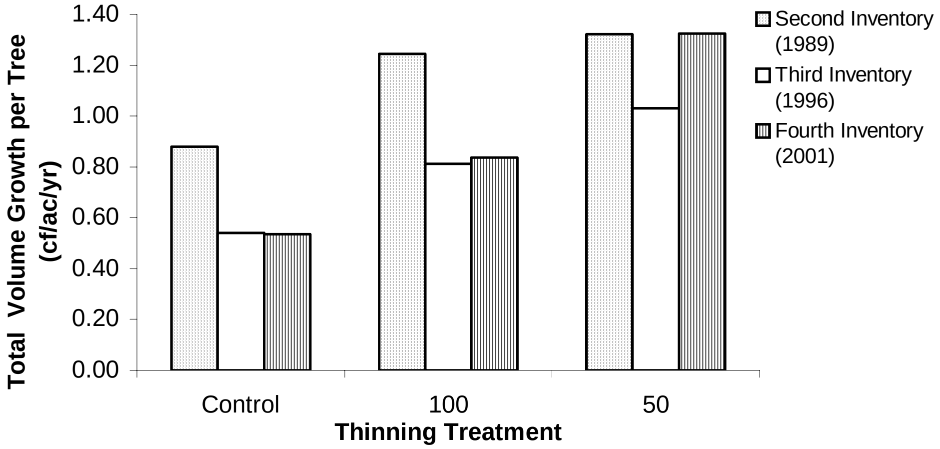

Figure 7—Total volume growth per tree for control and treatment plots.

An analysis of mean annual increment (MAI) showed that the MAI of the control plots peaked in 1985 and then declined while the MAI of the heavily thinned plots was still increasing in 2001. The MAI of the lightly thinned plots appeared to be leveling off (*fig. 8*). The next measurement should provide a clear indication of the MAI trend for these plots.

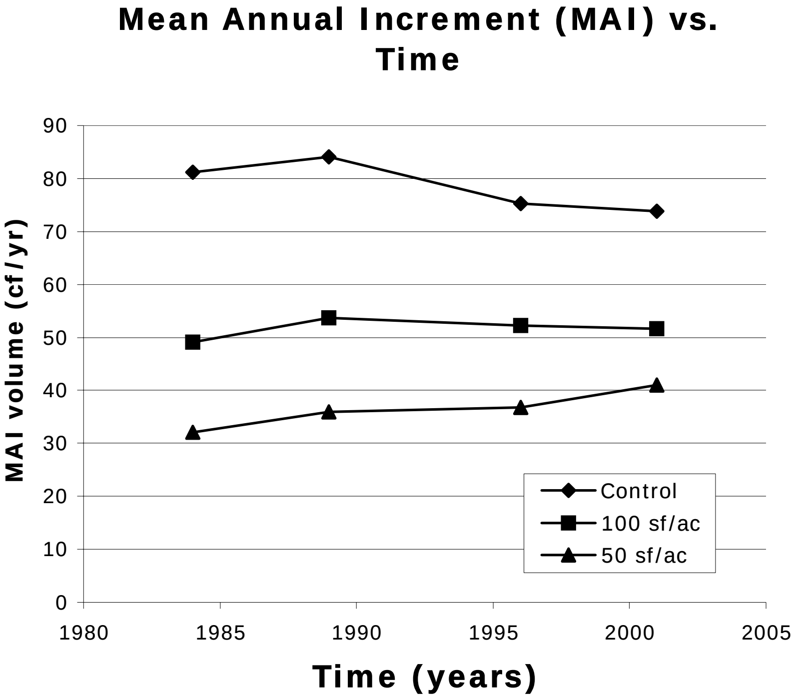

Figure 8—Mean Annual Increment over time.

Conclusions and Recommendations

Two major forest fires occurred during the 17-year interval that affected the study. Our data show that the denser, unthinned plots at the three burned sites sustained greater damage from fire than did the treatment plots at those sites. Management of the woodland forest can reduce losses from fire and, in general, protect the value of the resource.

By 2001, the control plots, study wide, had an average mortality of 93 trees per acre, compared to 14 trees per acre lost in the lightly thinned plots and 6 trees per acre lost in the heavily thinned plots. This was more dramatically shown in Site 1, which was heavily burned as a result of two fires during the 17-year period. The control plot lost 83 percent of its trees compared to the treatment plots, which lost an average of 26 percent. 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.

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 apparent in the five-year inventory and have only strengthened after 17 years of regrowth. Both basal area and total volume growth percentages were significantly greater in the thinned plots than the control plots. Average basal area per acre growth rates for the 17-year interval were 22 percent for treatment plots and 1 percent for control plots. In general, total volume growth rates were nearly three times as great in the treated plots compared to control plots.

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 per acre, per year). In fact, they averaged about 70 ft^3 per acre, per year. As of 2001, only the heavily thinned plots were increasing in MAI. This result is somewhat surprising given that tree MAI is expected to slow considerably in later years. This is significant as it relates to the potential for silvicultural practices to positively influence production of middle to mature-aged stands, which is important for the management of forests for commercial products.

As predicted in the last inventory report (Pillsbury and others 1998), ingrowth is now being seen. It should be noted that it has taken 17 years for ingrowth to appear. For the control plots, less than one-tenth of one percent of the number of stems per acre is attributed to ingrowth. For the lightly thinned plots, approximately 8 percent of the current total number of stems per acre is ingrowth and in the heavily thinned plots, 27 percent of the current stand is new ingrowth. Stumps were not protected in this study; however, we recommend that protection measures be taken in similar silvicultural practices to accelerate regrowth.

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Range Ecology

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Nutrient and Sediment Transport From a New Vineyard Within Oak Woodland[1]

Royce Larsen,[2] LynneDee Althouse,[3] Daniel Meade,[3] and Mark Battany[4]

Abstract

Water quality was investigated in the vicinity of Cuesta Ridge Vineyard, San Luis Obispo County, where drainages carry water from chaparral, oak woodland, and a new vineyard. Three drainages were instrumented with gauges above and below the vineyard for stage height and turbidity to assess the effectiveness of water quality protection measures at the Cuesta Ridge Vineyard. Water samples were taken during storm events and analyzed for pH, EC, nitrogen, phosphorus, and sediment concentrations. Erratic flow conditions may have made it difficult to identify differences above and below the vineyard. Water quality was good at all sites and data collected serves as baseline information for future study. Landform, geology, soil type, proximity to wetlands, and land use practices in the surrounding areas should be investigated to consider possible relationships with turbidity and nutrient concentrations.

Keywords: Buffers, rainfall, rangelands, turbidity, water quality.

Introduction

California vineyard acreage rapidly expanded during the last 20 years. Some of theses vineyards have been established in existing farm land, while other installations have converted rangelands and oak woodlands. There is minimal information available for land managers to help them use best management practices to protect water quality when these conversions are made (Dahlgren and others 2001). Available data are primarily qualitative. Data collection of runoff and erosion is not a straightforward or easy task; inputs from nearby waterways, variable adjacent land uses, and changes in land-use practices are confounding factors. Hence, qualitative data is abundant, relative to quantitative data.

Hajrasuliha and others (1998) followed the fate of nitrogen isotopes applied in the springtime as ammonium and nitrates to drip-irrigated table grapes in the San Joaquin Valley of California. They concluded that between 20 and 25 percent of the fertilizer was taken up by the vines during the growing season, while the vast majority remained within the rootzone at harvest, with nitrates moving deeper than ammonium. No assessment was made of nutrient movement with winter rainfall.

Bramley and Lanyon (2002) concluded that vineyards in Australia were inherently ‘leaky’ of nutrients below the rootzone, due to the tendency to over-fertilize because nutrients and irrigation are applied uniformly over vineyard blocks

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[2] UC Cooperative Extension. 350 N. Main Street, Suite B. Templeton, CA 93465. (805) 434-4106.

[3] Althouse and Meade, Inc. Biological and Environmental Services. 1875 Wellsona Road. Paso Robles, CA, 93446 (805) 467-1041.

[4] UC Cooperative Extension. 2156 Sierra Way, Suite C. San Luis Obispo, CA 93401. (805) 781-5940.

which themselves tend to be highly non-uniform in their soil conditions and vine growth.

Battany and Grismer (2000) investigated the effects of slope, cover and surface roughness on rainfall runoff and erosion using a rainfall simulator; they observed significant correlations between the slope, cover and surface roughness, and the total infiltration, runoff, sediment discharge, and average sediment concentration.

Slattery (2003), in his survey of Australian vineyard areas, concluded that many key Australian winegrape-growing areas have a moderate to high likelihood of nitrogen and phosphorous nutrient leakage out of the vineyard system, with the severity of leakage depending upon specific management practices in a given vineyard. The author recognized that the information required for determining the extent of nutrient loss was largely unknown, and suggested immediate research efforts to quantify these losses as they relate to best management practices such as cover cropping.

Stimson and O’Conner (2005) overviewed best management practices employed to reduce sediment loss in vineyards. They estimated by modeling with the RUSLE2 equation that management practices such as cover cropping should lead to significant reductions in sediment losses.

Ramos and Martinez-Casasnovas (2006) quantified the loss of nitrogen and phosphorous from a vineyard site in Spain. Even without considering the infrequent extreme runoff-generating rainfall events, the loss of nitrogen and phosphorous due to the smaller intensity runoff events was significant, being responsible for over 60 percent of the annual nutrient losses.

In a watershed-scale experiment that looked at pesticide movement rather than nutrients, Louchart and others (2001) looked at the movement of the pesticides diuron and simazine from vineyards to waterways; they noted fast movement of the compounds through bordering ditches, and concluded that the majority of the compounds likely re-infiltrated the soil through the same ditches.

Methods

We monitored the effects of a new vineyard on three streams. An above- and below-sampling design was used to monitor vineyard runoff. We were not able to obtain samples prior to the vineyard installation. Samples were collected near peak flow conditions during every storm event from 2000 to 2004. StatView SAS Institute Inc. (Version 5) was used for statistical analysis. The vineyard and sampling layout is shown in figure 1. This project was funded by the Regional Water Quality Control Board, Central Coast Vineyard Team, and Robert Mondavi Winery.

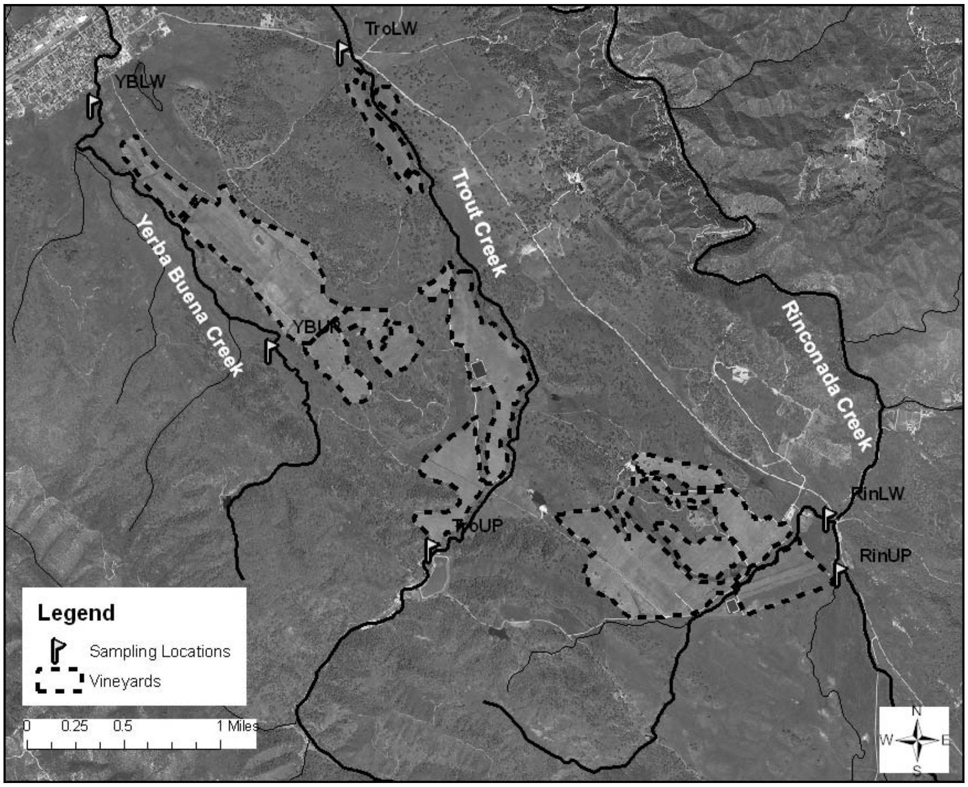

Figure 1—Water quality sampling locations on Yerba Buena, Trout and Rinconada creeks. Sampling sites were upper Yerba Buena (YBUP), lower Yerba Buena (YBLW), upper Trout (TroUP), lower trout (TroLW), upper Rinconada (RinUP) and lower Rinconada (RinLW).

The Cuesta Ridge Vineyard is a 900-acre vineyard, situated within a 14,000-acre ranch. The ranch is situated in a watershed characterized by headwaters with steep slopes and chaparral vegetation draining down through gentler slopes with oak woodland annual grassland vegetation type. It is located within the Paso Robles Hydrologic Area (HA 309.8) in San Luis Obispo County. Three major creeks, Rinconada, Trout and Yerba Buena (*fig. 1*), drain the vineyard to the Salinas River. This hydrologic unit is part of a salmon or steelhead trout Evolutionarily Significant Unit (ESU) (NOAA 2000).

Rinconada Creek runs along the north east side of the vineyard and has an un-named creek, which drains the vineyard. Trout Creek carries water from the chaparral in the Los Padres National Forest and several private summer residences, south of the ranch. All of Yerba Buena Creek upstream from the sample stations is within the ranch, draining the north side of Cuesta Ridge, east of Highway 101, before it flows through the town of Santa Margarita. Grazing is the dominant land use in the watershed.

Rinconada Creek watershed area is approximately 10,000 acres above the lower sampling site. There are approximately 8,000 acres of rangeland, with more than 1,000 acres farmed, above the upper sampling site. Trout Creek is approximately 6,400 acres above the lower sampling site, and 3500 acres above the upper sampling site. Yerba Buena Creek is approximately 2,800 acres above the lower sampling site, with 700 acres above the upper sampling site. Each of these watersheds contain approximately one third of the vineyard.

The operators and managers of the vineyard had a land management plan to protect water quality. The best management practices consisted of leaving adequate cover between vineyard rows and in buffer strips and biofilter areas. Cover crops were planted between rows using a variety of mixes to reduce erosion and compliment vine growth requirements. Cultivation was reduced to minimize the number of tractor passes per season. Roads were managed with soil cement, gravel, waterbars, mulch and the use of cover crops in low-use areas.

Rainfall was measured by two recording rain gages on the Cuesta Ridge Vineyard. Six permanent sampling sites, on three different streams, were established for collecting stream gage data and surface water samples. The sites were above and below the vineyard on Rinconada Creek, Trout Creek, and Yerba Buena Creek. The locations were labeled RinUP (Rinconada Creek above the vineyard), RinLW (Rinconada Creek below the vineyard), TroUP (Trout Creek above the vineyard), TroLW (Trout Creek below the vineyard), YBUP (Yerba Buena Creek above the vineyard) and YBLW (Yerba Buena Creek below the vineyard).

Turbidity: Turbidity was measured using an OBS3 sensor (D&A Instrument Co. 1991; Jordan 1996; Teti 1996). The infrared signal was emitted every 15 minutes. Data were stored on a Hobo datalogger and the voltage converted to NTUs (range set at 0-250 during 2001 to 2002 and 0-725 NTU from fall 2002 to 2004).

Suspended Sediment: One bottle was collected for each location during each sampling session. Suspended sediment samples were taken using a DH48 integrating sediment sampler and submerged in the fastest flow water with the nozzle pointed upstream. The bottle was slowly raised and lowered to collect water from the entire water column, taking care not to disturb bottom sediments. Samples were suction-filtered and dried at 45°C for two days.

Nutrient: Grab samples were collected in opaque plastic bottles. Samples were frozen and shipped FedEx within two weeks after sampling. Nutrients, EC, pH were analyzed at the DANR laboratory at UC Davis.

Stage Height: Stream height was measured with an AG5 Aquatape (Consillium). Data were collected every 15 minutes and stored on a Hobo datalogger. Voltage readings were converted to centimeters. Lower Rinconada was equipped with a 12-foot aquatape. The other sites were initially instrumented with 8-foot tapes. In the fall of 2001, upper Rinconada and lower Trout were equipped with 12-foot aquatapes, due to storm events in February 2001 that swamped the original installations at those two sites. The aquatapes were installed in steel pipes (old oil field pipes) acting as still wells anchored to the bank. Each still well was installed so the aqua tape was below the stream bed surface.

In addition to automated sampling, field measurements were taken each time the site was visited for grab samples. The still wells were outfitted with stream gages measuring in centimeters.

Velocity: Stream velocity was measured with a FP101 hand-held flow meter (Global Water). The units were measured in feet/second. Several measurements were taken at each site, at 1/3 and 2/3 depths, the results were averaged.

Results

Rainfall

Rainfall was highest (24.2 inches) in 2000 to 2001 (01-02), a slightly below average rainfall year (*fig. 2A*). The average recorded rainfall is approximately 30 inches. Stream flow began in January 2001, and the largest storm events were in March of the same year. Rainfall during subsequent years was well below average: 9.8 in 01-02; 18.8 in 02-03; 11.3 inches during 03-04 (Figure 2B-D). Low amounts and timing of rainfall equated to very low stream flow, rarely exceeding baseflow conditions

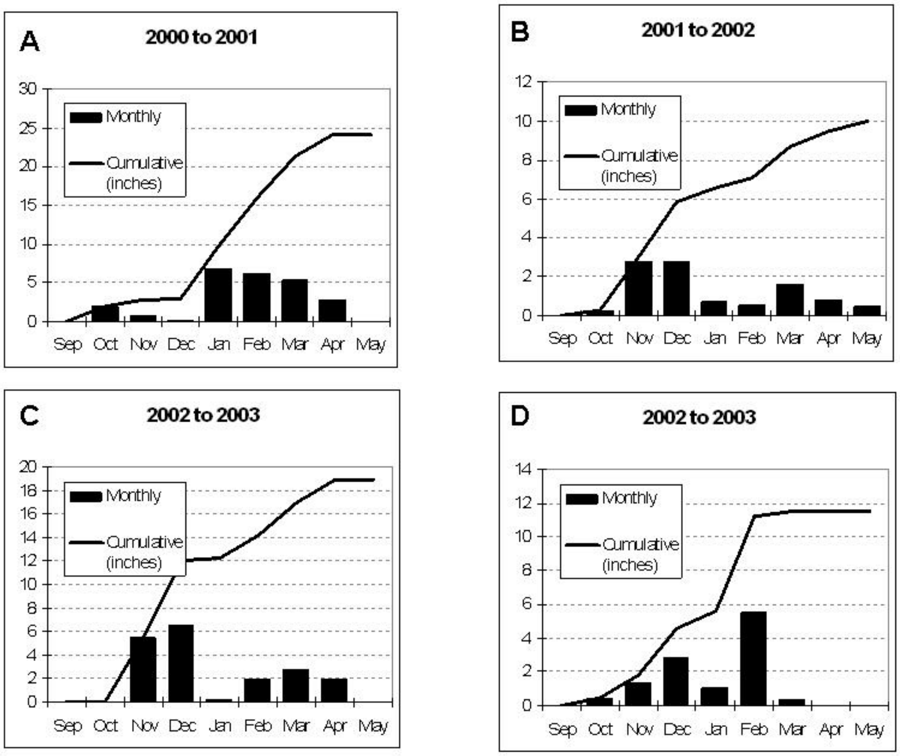

Figure 2—Cumulative (line) and monthly (bar) rainfall is shown for 2002 to 2001 (A), 2001 to 2002 (B), 2002-2003 (C), and 2003 to 2004 (D).

Turbidity and Suspended Sediment

Maximum turbidity was over 700 NTU in Rinconada Creek, above and below the vineyard. Moderate turbidity was over 200 NTU in Trout Creek, above and below the vineyard. Yerba Buena Creek maximum turbidity was never over 100 NTU. Upper Yerba Buena, above the vineyard was twice the value of the Lower Yerba Buena site.

Suspended sediment grab sample values confirm the trend monitored by the automated turbidity sensor. The highest sediment measured was in Rinconada Creek, over 7,000 mg/L. The highest sediment in Trout Creek was between 2,700 and 3,700 mg/L. Yerba Buena high sediment values were between 780 and 1,100 mg/L. See the high, low and average values for each sampling site in table 1. There were no significant differences (p=.21) between sediment concentrations above and below the vineyard, see figure 3. This indicates that the vineyard did not increase sediment loading above that which was already in the streams coming into the vineyard.

Table 1—*Turbidity was measured every 15 minutes at six locations. Suspended sediment grab samples were taken during and after storms. High values are shown in bold.*

Constituent	Units	RinLW	RinUP	TroLW	TroUP	YBLW	YBUP
Turbidity High	**NTU**	**718**	**720**	**281**	**255**	**38**	**64**
Turbidity Low	NTU	2	1	1	1	1	1
Turbidity Average	NTU	360	360.5	141	128	19.5	32.5
Sediment High	**mg/L**	**7333**	**6952**	**2736**	**3740**	**782**	**1099**
Sediment Low	mg/L	0	0	0	0	0	0
Sediment Average	mg/L	3667	3476	1368	1870	391	549

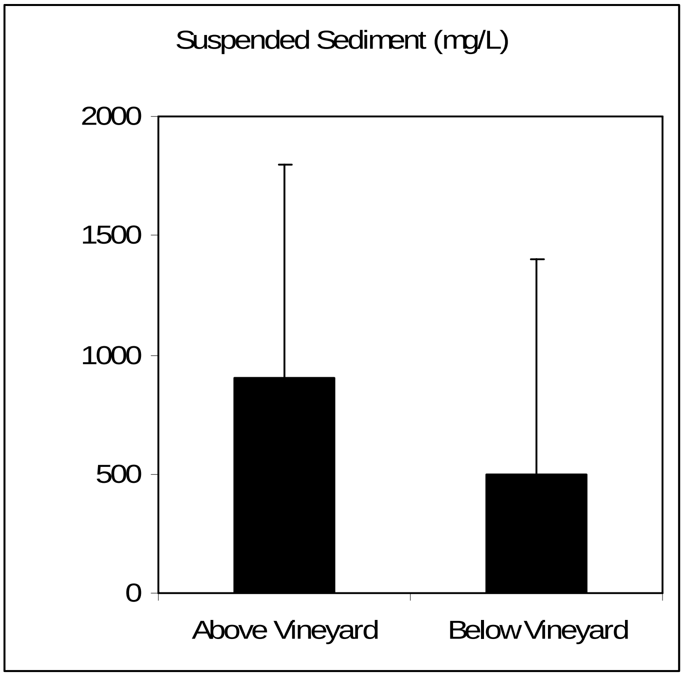

Figure 3—Suspended sediment (mg/L) was sampled above and below vineyards. There was no significant difference between above and below vineyard sediment concentrations. (n=67 above vineyards; n=91 below vineyards).

pH

The pH varied from 6.4 in Lower Yerba Buena Creek to 8.7 in lower Rinconada Creek. See high, low and averages for the pH values in table 2.

Table 2—*pH was measured at the DANR lab prior to nutrient analysis.*

Constituent	**Units**	**RinLW**	**RinUP**	**TroLW**	**TroUP**	**YBLW**	**YBUP**
High	Units	8.7	8.5	8.7	8.2	8.1	8
Low	Units	6.8	7	6.8	6.8	6.4	6.5
Average	Units	7.8	7.8	7.8	7.5	7.3	7.3

Electrical Conductivity

The highest EC recorded at four sites was 0.7 mmhos/cm, and the low at all sites was 0.1 mmhos/cm. See the high, low and average EC values in table 3.

Table 3—*EC was measured at the DANR lab prior to nutrient analysis.*

Constituent	**Units**	**RinLW**	**RinUP**	**TroLW**	**TroUP**	**YBLW**	**YBUP**
High	mmhos/cm	0.7	0.7	0.7	0.6	0.7	0.3
Low	mmhos/cm	0.1	0.1	0.1	0.1	0.1	0.1
Average	mmhos/cm	0.4	0.4	0.4	0.4	0.3	0.2

Nutrients

Total Kjeldahl nitrogen was highest in upper Rinconada and Trout Creeks, 27 and 25 ppm, respectively. The highest values at the other sites varied from 11 to 22 ppm. High values at all sites were over 10 ppm. Low values were between 0.1 and 0.3 ppm TKN.

Ammonia concentrations were highest in Rinconada Creek 0.6 ppm and never higher than 0.2 ppm at all other sites. There were periods in which no ammonia was detectable at all sites.

Nitrate concentrations were highest in Lower Yerba Buena 2.1 ppm. High values in Rinconada were 1.5 and 1.3 ppm. Trout Creek and upper Yerba Buena never exceeded 0.6 ppm. A small amount of nitrate 0.1 ppm was always detected in the lower drainages, and there were periods when no nitrate was detectable in the upper drainages.

Total phosphorus was highest in Rinconada Creek, 12.8 ppm in lower Rinconada and 10.4 ppm in upper Rinconada. High concentrations of phosphorus at all other sites were between 1.2 and 5.3 ppm. Low concentrations varied from 0.1 to 0.3 ppm. See high, low and average values for TKN, NH_3, NO_3, Psol, Ptot in table 4.

There were no statistical differences ($p=0.25$) for TKN above and below the vineyard. This indicates that the vineyard did not increase the TKN loading from other sources already in the streams, figure 4.

Table 4—*Nitrogen (TKN, NH_3, NO_3) and Phosphorus (P_{sol} P_{tot}) were analyzed by DANR lab.*

Constituent (units are ppm)	Units	RinLW	RinUP	TroLW	TroUP	YBLW	YBUP
Nitrogen – Total Kheldahl (TKN)	**High**	**18.1**	**26.8**	**10.8**	**24.8**	**21.3**	**15.8**
	Low	0	0	0	0.1	0.3	0.3
	Average	2.9	2.4	1.3	4.4	4.1	4.3
Ammonia (NH_3) – N	**High**	0.6	0.6	0.2	0.1	0.1	0.1
	Low	0.0	0.0	0.0	0.0	0.0	0.0
	Average	0.6	0.6	0.2	0.1	0.1	0.1
Nitrate (NO_3) – N	**High**	1.5	1.3	0.6	0.5	2.1	0.5
	Low	0.0	0.0	0.0	0.0	0.0	0.0
	Average	0.3	0.2	0.2	0.2	0.5	0.2
Phosphorus, soluble (P_{sol})	**High**	0.3	0.3	0.6	0.5	0.5	0.2
	Low	0	0	0.16	0	0	0
	Average	0.1	0.1	0.3	0.3	0.2	0.1
Phosphorus, total (P_{tot})	**High**	12.8	10.4	2.4	5.3	2.2	1.2
	Low	0.0	0.0	0.0	0.0	0.0	0.0
	Average	0.9	0.6	0.6	1.1	0.7	0.3
n =		38	39	40	18	16	11

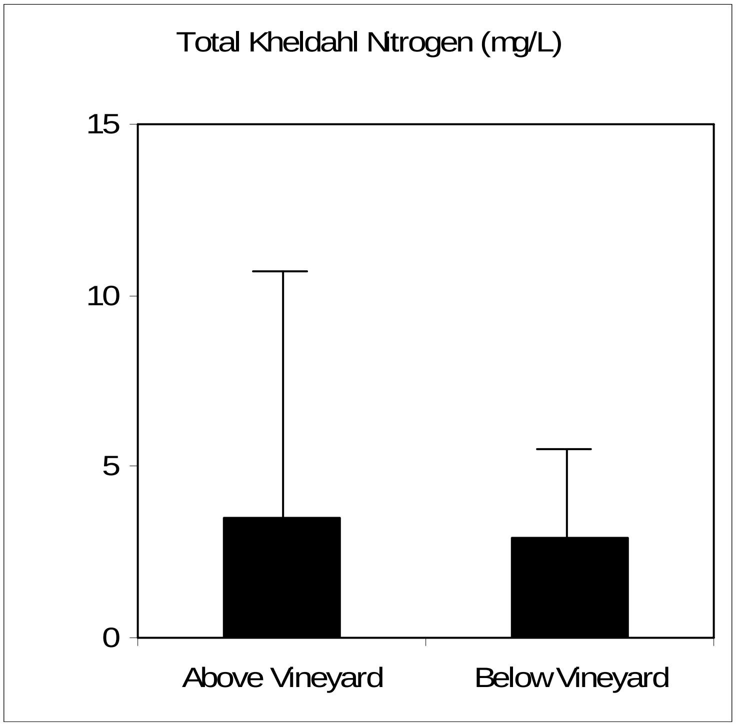

Figure 4—Total Kheldahl nitrogen was measured above and below vineyards. Although highly variable, there was no significant difference between sites.

Stage Height

Upper Rinconada Creek was over 8 feet deep and the lower site over 9 feet deep in March 2001. Upper Trout Creek overtopped the banks, greater than 6 feet deep during that large storm. Lower Trout Creek swamped the 8-foot stillwell, and it needed to be moved downstream to a safer location. Upper Yerba Buena Creek overtopped the banks at 3.5 feet, which occurred in March 2001. Lower Yerba Buena Creek exceeded 5.5 feet deep, as it flooded the channel banks during this same storm. This large storm created many problems with the aquatapes and stage height measurements, which required corrections. By fall of 2002, those corrections had been made. Lower trout creek site was moved downstream to a wider part of the channel, and upper Trout Creek station was moved from the north to the south side of the creek because over 4 feet of debris and gravel had accumulated on the north bank. The upper Trout Creek cross-sectional area was reduced by 45 square feet during the March 2001 storm event.

Discussion

Suspended sediment movement is directly related to storm events in these streams. For demonstration stage height and sediment concentrations are shown for a large storm event December 16-22, 2002. Figure 5 graphically illustrates turbidity, stage height, and daily rainfall in Rinconada Creek during this storm.

Overall, there were no significant differences in sediment concentrations. The flow conditions may have contributed to this. Rainfall between 2001 and 2004 was below average each year. Our results are limited by infrequent rainfall events sufficient to produce storm flow in the three drainages. From January 2001 to March 2004, there were only seven storms that produced measurable stormflow at all six sites. Rinconada Creek was dry in the summer of 2002 and 2003. Base flow resumed in the fall. Upper Trout Creek only had surface flow after large storm events. Lower Trout Creek had base flow through the entire study period. Trout Creek is aggrading due to post-fire gravel, debris, and sediment transport from the Los Padres National Forest. Upper Yerba Buena Creek flowed during the winters of 2001 and 2002. It only flowed during, and shortly after large storm events, in 2003 and 2004. Lower Trout Creek had base flow through the entire study. Upper and Lower Rinconada Creek began to flow in the fall as temperatures began to drop. Yerba Buena Creek only flowed during and after storm events. The most ephemeral of the sites is Upper Trout Creek, where the bed load is a thick layer of gravel, and water flows under the stream bed for long periods of the year.

Water quality in Yerba Buena Creek was generally better than in Trout Creek and Rinconada Creek. This may be due, in part, to the smaller size of the Yerba Buena watershed relative to the other study sites. Yerba Buena is one third the size of Rinconada and less than half the size of Trout Creek within the study area. Yerba Buena Creek is entirely within the ranch boundaries and the watershed above the vineyard in is good ecological condition with grazing being the only use.

Rinconada Creek had the highest turbidity of the three study drainages. The suspended sediment measured for Rinconada Creek was three times higher than Trout Creek and over 14 times higher than Yerba Buena Creek. High sediment loads measured 7,000 mg/L in Rinconada Creek, which was very similar both above and below the vineyard indicating the vineyard did not contribute to increased sediment loads. The land uses and the number of dirt roads may contribute to the amount of turbidity in Rinconada Creek, although no measure of roadways and farming activities was made during this study. There was 1,400 to 1,900 mg/L in Trout Creek and 400 to 500 mg/L in Yerba Buena Creek. In all cases, the vineyard did not add increased sediment loads. In some cases, the sediment concentrations were lower after the water passed through the vineyard.

Water quality values in Trout Creek was typically in the mid-range between Yerba Buena Creek and Rinconada Creek. Trout Creek had less sediment than Rinconada, and more than Yerba Buena. Trout had total phosphorus and nitrogen between the values of Yerba Buena and Rinconada Creek.

Ammonia, nitrate, and soluble phosphorus concentrations were very low. Variations observed may be influenced by factors that were not measured in this study. Landform, geology, soil type, proximity to wetlands, and land use practices in the surrounding areas should be investigated to consider possible relationships with turbidity and nutrient concentrations. The data serve as baseline information given the unusual flow patterns. Each of the three drainages showed high suspended sediment and low nutrients during major storm events between 2001 and 2004.

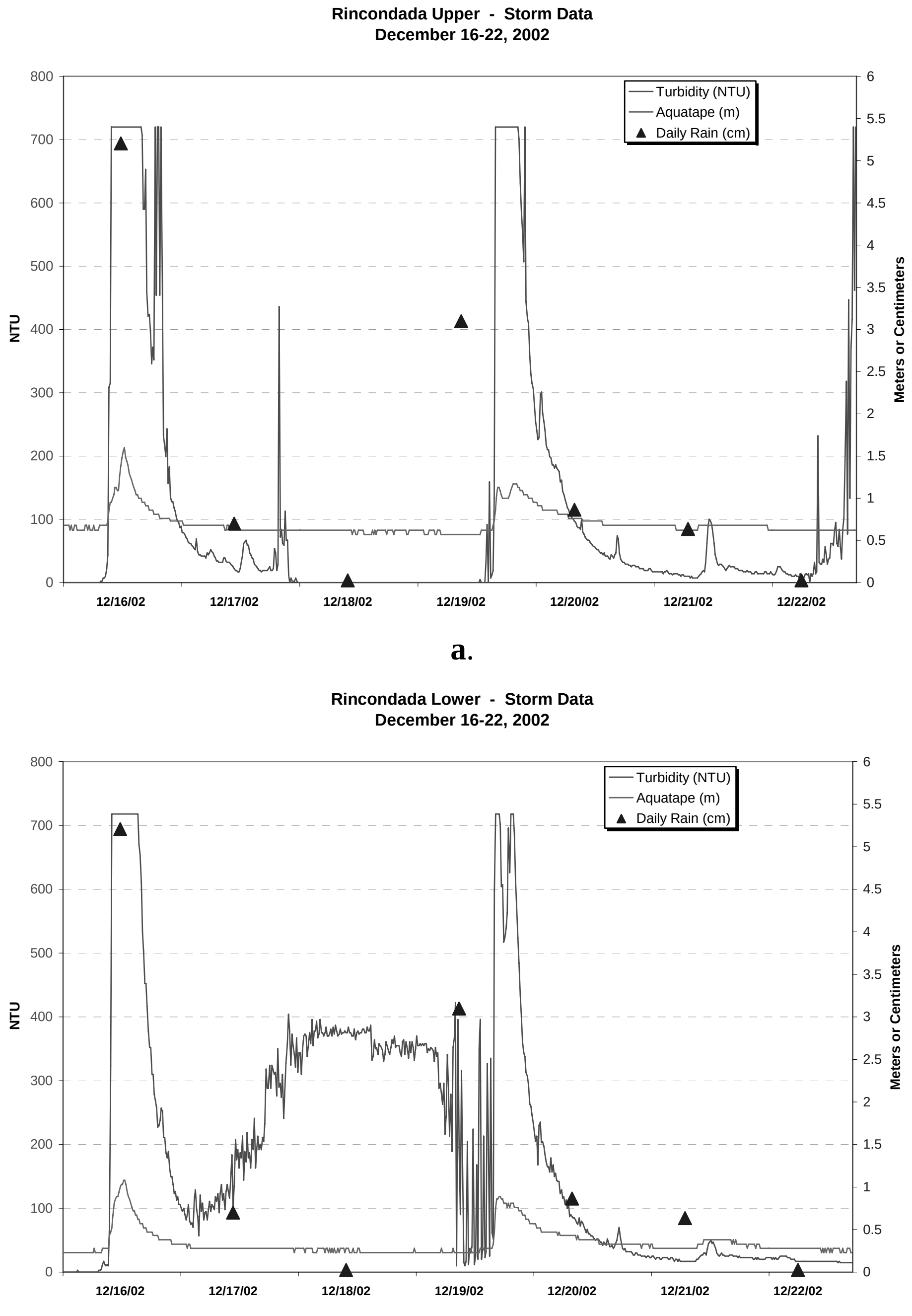

Figure 5—Upper and lower Rinconada Creek (a and b) show similar stream flow characteristics to the other two drainages. Turbidity is generally high after several inches of rainfall. The long period of turbidity indicated December 17 to 19 (arrow) is probably watercress or other vegetation clinging to the turbidity sensor.

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Oak Woodland Vegetation Dynamics: A State and Transition Approach[1]

Melvin R. George[2] and Maximo F. Alonso[2]

Abstract

California's oak-woodlands are a complex, often multi-layered mosaic of grassland, shrubland, and woodland patches. While soil type and depth, topography, aspect, and geological substrate influence the distribution of these patches, disturbance and biological interactions are also important determinants of the patchy distribution of these plant communities. Fire intensity and frequency can change the structure of these patches, while grazing can affect the speed of the species replacement. Different re-establishment strategies of woody species interacting with prevailing weather following disturbance can also produce changes in the plant community composition at the patch level which are often smaller than a soil mapping unit or an ecological site. While our knowledge of vegetation dynamics in the oak-woodlands is not great, what we do know, or can reasonably hypothesize, is being organized into a format that is sensible and accessible to natural resource managers. State and transition models have been proposed as a format for organizing the complex body of knowledge and concepts describing vegetation dynamics in rangeland ecosystems. Natural and man-caused vegetation change can be incorporated into these models. In this review paper, we will describe oak-woodland vegetation dynamics using a state and transition format.

Keywords: Oak-woodlands, state and transition models, succession, vegetation dynamics.

Introduction

USDA Natural Resources Conservation Service is developing ecological site descriptions for the nation's rangelands (NRCS 1997). An ecological site is a distinctive kind of land with specific physical characteristics that differs from other kinds of land in its ability to produce a distinctive kind and amount of vegetation. Soils with similar properties that produce and support a characteristic plant community are grouped into the same ecological site. Ecological site descriptions outline physiographic, climatic, hydrologic, soil, vegetation and wildlife characteristics of the site. Part of the ecological site description is a state and transition model that describes vegetation dynamics on the site. The purpose of this report is to describe the on-going development of state and transition models for the oak-woodlands. In this report. we will 1) review state and transition models, 2) review vegetation dynamics that will be embodied in transition descriptions, 3) briefly report on survey and analysis procedures used to determine vegetation states, and 4) present an example of an oak-woodland state and transition model.

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[1] An abbreviated version of this paper was presented at the Sixth California Oak Symposium: Today's Challenges, Tomorrow's Opportunities, October 9-12, 2006, Rohnert Park, California.

[2] [2] Specialist and Graduate Student respectively, University of California, Plant Sciences, One Shields Avenue, 1210 Plant and Environmental Sciences Bldg., Davis, CA 95616-8780. e-mail: mrgeorge@ucdavis.edu, malonso@ucdavis.edu.

State and Transition Models

Traditional theories of plant succession leading to a single stable end point (climax community) do not adequately describe non-equilibrium vegetation dynamics characterized by multiple successional pathways and multiple stable endpoints. Westoby and others (1989) proposed state and transition models as practical formats for describing multiple successional pathways, multiple steady states and discontinuous and irreversible transitions (Stringham and others 2003). The USDA NRCS adopted state and transition models for describing traditional succession dynamics, as well as non-equilibrium dynamics (USDA 1997).

A state and transition model includes 1) a catalog of possible alternative vegetation states associated with an ecological site and a catalog of transitions from one state to another. The level of detail may range from specific experimental results collected on the ecological site to general science-based or experience-based knowledge of ecological site response to natural or human-caused disturbances. Westoby (1989) defined a state as an alternative, persistent vegetation community that is not simply reversible in the linear successional framework. Stringham (2003) defined a state as a recognizable, resistant and resilient complex of the soil base and vegetation structure. Transitions are the pathways between states. Transitions are often triggered by natural or human-caused disturbances. Transitions may occur quickly, as with a fire or flood, or more slowly in response to repeated stress such as grazing or drought.

Oak-Woodland Vegetation Dynamics

Oak-woodland transitions are based on scientific literature and the experience of scientists and managers. While fire plays a major role in oak-woodland succession, life history traits of the oak-woodland vegetation contribute to the vegetation structure’s resistance to change and to the potential for multiple successional pathways.

Fire is a normal disturbance in California’s oak-woodlands. Cooper (1926) observed a coast live oak stand in Santa Clara County and concluded that an oak savanna requires disturbance and, in the absence of heavy grazing or frequent fires, live oaks and bird-dispersed shrubs will increase. Foothill pine and ceanothus shrubs have increased in an ungrazed (natural area) oak-woodland at the San Joaquin Experimental Range, which has not burned since 1929 (Woolfolk and Reppert 1963). In an extensive study of the relationship between vegetation type, substrate, and disturbance, Wells (1962) concluded the original vegetation of the San Luis Obispo area was broad-schlerophyll forest on all types of substratum. In his view, anthropogenically caused fires (starting with Native Americans and continuing with European settlers) and grazing eventually destroyed this forest, leading to the currently observed mosaic of grassland, shrubland, and forest (Hamilton 1997). According to Callaway and Davis (1993) California’s oak woodlands are in dynamic equilibrium with other plant associations, and depending on their location and disturbance regimes, they can be converted into grasslands as well as derived from coastal sage scrub and chaparral (Callaway and Davis 1993).

Life histories and life history traits of oak-woodland vegetation greatly influence the course of succession. Different rates of survival, tolerances to stresses and disturbance and abilities to compete lead to different community structures and rates of succession that result in the potential for multiple successional pathways, resulting in multiple stable states (Egler 1974; Drury and Nisbet 1973; Grime 1974, 1979; Connell and Slatyer 1977). The understory layer, dominated by annuals, produces a large, dense and diverse seed bank (Rice 1989a). Annually, some portion of the seedbank germinates and completes its life cycle in one growing season. Competition during germination, establishment and growth mediated by weather, microclimate and nutrients greatly influences the species composition of this layer and its competitive ability (Rice 1989b). The competitive ability of annuals for moisture and other resources contributed to the loss of the former native perennial understory and adjacent grassland. More recently, competition for soil moisture by annuals has been shown to be an important contributor to poor blue oak regeneration (Gordon and others 1989).

The tree layer is dominated by long-lived oaks (White 1966) that vary in their fire resistance and resprouting capacity (FEIS 2006). All produce acorns, often in pulses every several years. Germination and seedling survival to the sapling state are inhibited by the annual dominated understory (Gordon and others 1989, McCreary 2001). The shrub layer is characterized by two functional groups: 1) species that resprout from surviving sub-surface stems and roots following fire, and 2) species that are stimulated to germinate by fire or smoke. Resprouting species maintain live biomass below ground and recover rapidly following fire. Recovery is slower for non-resprouting species and depends on fire interval and the age of maturity. Species with fire-stimulated germination show a peak growth phase immediately following a fire and then a decrease in establishment and growth due to their low competitive ability (Pausas 1999).

Long-lived species provide the community with a great deal of inertia against vegetation change. Fire rejuvenates shrub stands. Without fire, the above ground portions of the shrub layer eventually become decadent and die. According to Hanes (1971), 60-year-old chamise and ceanothus stands are often decadent. Without fire for more than 70 years, ceanothus shrubs in the natural area at the San Joaquin Experimental Range are decadent and dying. The longevity of the below-ground portions of resprouting species is not known, but studies in Europe suggest that *Quercus ilex* root systems can be hundreds or thousands of years old (Pausas 1999). Consequently, establishment of long-lived species may not be related to current climatic conditions.

The oak-woodlands of California’s coast range and Sierra Nevada foothills are often a mosaic of grassland, oak-woodland, and shrubland. California’s central coast is dominated by a mosaic of grassland, oak-woodland, coastal sage scrub, and chaparral (Wells 1962, Griffin 1977, Heady 1977, Mooney 1977). In some locations, these mosaics have been correlated with geological substrate (Cole 1980) and soil characteristics (Harrison and others 1971). However, other researches have found each of these vegetation types on most soil depths, slopes, aspects and all geological substrates, suggesting that disturbance and/or biological factors are important determinants of the patchy distribution of these vegetation types on California’s central coast (Wells 1962, Callaway and Davis 1991).

Oak-Woodland States

Methods

States describe alternative vegetation structures associated with an ecological site. To determine vegetation structures on oak-woodland ecological sites, vegetation was surveyed along 455 transects distributed on widespread soil series in Major Land Resource Areas (MLRA) 15 (294 transects) and 18 (161 transects) during the 2004 and 2005 growing seasons. These transects were 100 m in length and were used to determine understory productivity, canopy cover, and tree and shrub density.

To identify potential states, we examined species composition differences among the transects. For this purpose, we conducted non-metric multidimensional scaling (NMDS) with four ordination axes using R, version 2.2.1. A dissimilarity matrix using Manhattan distances was calculated from the species abundances in each transect. The distances in the ordination space represent community similarity (ter Braak 1995). The correspondence of the ordination diagram to the similarity distances is described by a stress value where 0 is a perfect fit (Kneitel and Chase 2004). The result for the four ordination axes was used to generate the cluster of vegetation types. The cluster analysis was conducted in JMP IN 5.1.

Results

Woody species were found in 267 of the 455 transects, and were grouped in 15 clusters. From a total of 54 woody species, only 14 were present in more than 10 transects: *Adenostoma fasciculatum, Aesculus californica, Arctostaphylos sp., Baccharis pilularis, Ceanothus cuneatus, Pinus sabiniana, Quercus agrifolia, Quercus douglasi, Quercus garryana, Quercus kellogii, Quercus lobata, Quercus wislizenii, Toxicodendron diversilobum, and Umbellularia californica*. The 15 clusters were classified into 11 oak classes (Allen-Diaz 1989): 1) Blue-Oak/Grass 2) Blue Oak-Interior Live Oak/Grass, 3)Blue Oak-Coast Live Oak/Grass, 4) Interior Live Oak-Blue Oak-Foothill Pine, 5) Coast Live Oak-Blue Oak/Grass, 6) Coast Live Oak/Sagebrush/Grass, 7)Coast Live Oak-California Bay/Toyon-Scrub Oak, 8) Valley Oak-Grass, 9) Valley Oak-Coast Live Oak/Grass, 10)Mixed Oak/Grass, and 11)Mixed Oak-Black Oak/Grass. These classes will be used to describe potential vegetation states in the oak woodlands.

Oak-Woodland States and Transitions: An Example

Models currently being developed describe the states and transitions of fire-adapted oak-woodland communities (Appendix A). Under normal fire regimes, we expect the tree layer (oaks and other species) to survive the fire more or less intact. It is the shrub and herbaceous layer that is most affected by the fire. In this situation, we expect a post fire succession in which some annuals rapidly germinate, establish and dominate much of the understory, setting seed and completing their life cycle as the dry season begins. Shrub replacement is a slower process. While resprouting shrubs may rapidly re-occupy the site, shrubs with seeds that are stimulated to germinate by fire, such as many species of ceanothus and manzanita, will require several years to re-dominate former patches or form new patches. In the state and transition models, this sequence is the normal or reference state for several oak-woodland ecological sites. Under catastrophic fire associated with long fire return intervals this normal sequence may be altered in several ways. One or more oak species may be lost or substantially reduced on the site. The seed bank may be reduced by the fire. In the extreme, this may result in loss of trees or shrubs or a slower recovery.

Following a fire, oak-woodland communities are characterized by standing live plants and by a seed bank/vegetative bud bank of species that survived the fire. This species composition is augmented by migration of propagules from adjacent undisturbed areas. The species represented in the seed/bud bank are characterized by different growth rates, different live histories and different longevities. Functionally, many of these species are annual herbaceous grasses and forbs that complete their life cycle in one year; some are shrubs that resprout while others have deposited seeds that are stimulated to germinate by heat. Most oak trees resprout following fire and all produce seeds (acorns).

Following fire, complex species interactions on variable soil and geologic substrates may result in the mosaic of vegetation types. Callaway and D’Antonio (1991) found that seedlings of coast live oak were spatially associated with shrub communities, and that survival of seedlings was improved by shrub cover. They suggested that a sequence of nurse plant facilitation and oak-shrub competition may affect patterns and boundaries of these communities. Chaparral species have been reported to out-compete coast sage scrub species for light and to replace them successionally (McPherson and Muller 1967, Hanes 1971, Gray 1983). Coastal sage scrub and chaparral shrubs suppress grass species (Muller and del Moral 1966, Bartholomew 1970, Halligan 1976), and some of the same grass species suppress growth of oak seedlings (Gordon and others 1989). These types of biological interactions, acting in concert with natural disturbance, and variation in topography and substrate, may produce complex transitional changes among community mosaics along the central coast of California.

While fire has an immediate and sometimes catastrophic effect on oak-woodland communities, grazing effects are slow and relentless. In a few studies that compare post fire recovery with and without livestock or deer grazing/browsing, recovery is slower when grazers/browsers are present (McBride and Heady 1968, Johnson and Fitzhugh 1990, Callaway and Davis 1993).

Besides changing fire intervals, managers can alter the course of succession through the practices that they apply. Type conversions in which woody plants were permanently removed using mechanical and chemical controls are the extreme case in which woodlands have been converted to grasslands. Firewood cutting can also convert woodland to a savanna or grassland. Frequent fire (short return intervals) and goat grazing can effectively remove shrubs from the shrub layer, producing an oak-savanna. Sometimes these changes are irreversible, resulting in new pathways of change and new stable states.

Research Needs

There is a great deal about oak-woodland vegetation dynamics that is not known. Life histories and life history traits are poorly known. Competition is a major driver of changes in vegetation structure but has not been adequately studied. How will these plant communities respond to long-term fire suppression, climate change, and biological invasions? What are the transitions that lead to conversions between grasslands, shrublands, savannas, and woodlands. What are the rates of these transitions. At what thresholds are these transitions no longer reversible? There are many questions.

Studies of vegetation change involve indirect and direct methods. Indirect methods involve inference of successional patterns based on data or observations taken at a single time during a successional sequence. For communities with long-lived species, this is often the method of choice.

Direct methods of study are based on observation of succession on permanent plots or through the use of historical documents that give details of former vegetation. Direct observation and study of succession in plant communities that include long-lived species is an intergenerational endeavor. Thus there is a need to initiate and maintain long-term studies of vegetation change in California's oak-woodlands and associated communities. The Vegetation Type Mapping (VTM) plots initiated by Weislander in the 1920s and recently cataloged by Kelly and others (2005) represent a unique opportunity to estimate vegetation change over the last century.

The results of this project will be incorporated into ecological site descriptions and, following peer review, will become part of the Ecological Site Information System (http://esis.sc.egov.usda.gov) maintained by USDA Natural Resources Conservation Service.

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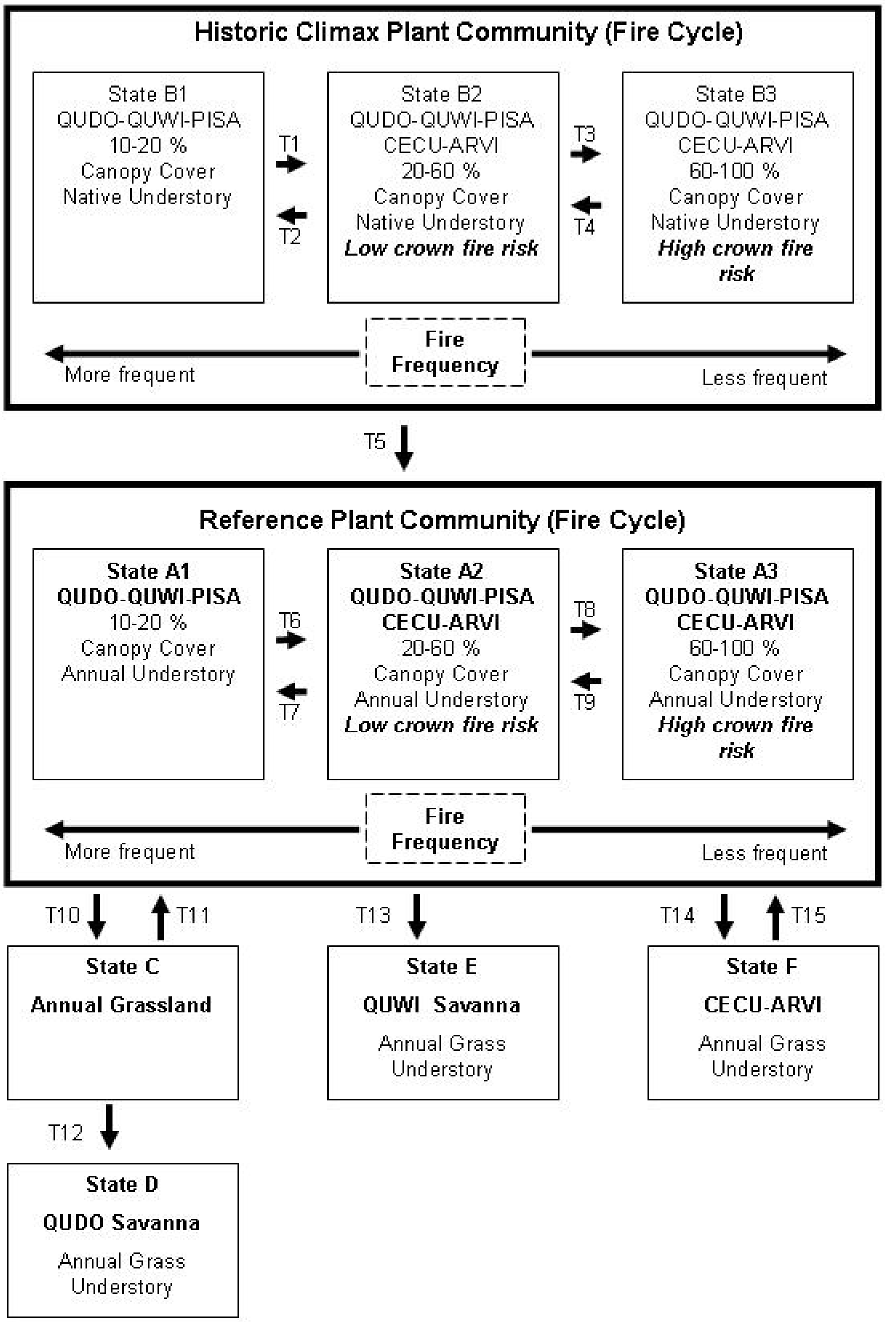
Appendix A.

State and Transition Model for the woody layers of a granitic soil



State Descriptions

State A1: Savanna community (10 – 20 percent canopy cover) consisting of a blue oak, interior live oak, and foothill pine tree layer and few or no shrubs. Blue oaks are fire resistant and evolved under low-severity grassland fires. Interior live oak is sensitive to fire but resprouts vigorously following most fires. Foothill pine is sensitive to moderate or intense fires but is increasing due to fire suppression. Ceanothus and manzanita seeds germinate following fires. Understory is generally dominated by annual grasses and forbs of Eurasian origin. Allen Class: Blue Oak-Interior Live Oak/grass.

State A2: Savanna community (20 – 60 percent canopy cover). Allen Class: Blue Oak-Foothill Pine/Whiteleaf Manzanita/Grass or Blue Oak-Foothill Pine/Wedgeleaf Ceanothus/Grass.

State A3: Woodland community (canopy cover >60 percent). Allen Class: Blue Oak-Foothill Pine/Whiteleaf Manzanita/Grass or Blue Oak-Foothill Pine/Wedgeleaf Ceanothus/Grass.

States B1, B2, and B3: Historic climax plant community assumed to consist of tree and shrub layers similar to those in State A. Perennial-dominated understory species composition is not known. States B1, B2 and B3 assume that native annual and perennial grasses and forbs were common in the understory of the tree and shrub layer of these oak-woodland ecosystems.

State C: Annual grass- and forb-dominated grassland. Soil quality, especially fertility, declines following tree removal.

State D: Blue oak savanna. Artificially regenerated oak woodland with an annual grass understory. Allen Class: Blue Oak/Grass or Blue Oak-Understory Blue Oak/Grass.

State E: Live oak savanna. Live Oak dominated savanna. Allen Class: Live Oak/Grass

State F: Ceanothus and/or manzanita chaparral.

Transition Descriptions

T1-State B1 to State B2: Under natural fire frequencies shrub and tree canopy cover increases toward State B2 following fire.

T2-State B2 to State B1: Natural fire frequencies estimated to be 25 years; maintains an oak savanna with a few shrubs and an herbaceous understory. More frequent burning can result in a savanna free of shrubs and understory trees. Application of mechanical and/or chemical brush control practices can result in a similar transition.

T3-State B2 to State B3: Prolonged periods without fire result in increased shrub and tree canopy cover to the point where the savanna is classified as woodland. Increasing ladder fuels increase the chances of a high intensity crown fire.

T4-State B3 to State B1 or B2: Burning woodlands with dense shrub layers results in removal of most shrub and understory tree canopy. In extreme cases, this transition could return from State B3 to State B1. Implementation of mechanical or chemical brush control practices can result in a similar transition.

T5-State B to State A: Invasion by exotic annual species, yearlong continuous grazing, drought, fire suppression and cultivation reduced or destroyed the native perennial grass and forb component of the historic climax plant community. Apparently an irreversible transition in a time frame relevant to management. Restoration of native perennial herbaceous vegetation is a recurring management objective that has been largely unsuccessful. Researchers, managers and citizens groups have been unsuccessful at reversing the loss of native perennial grasses. Competition from invasive annuals and long dry summers apparently are insurmountable. Annual grasses and forbs are more competitive for soil moisture than native perennials reducing oak seedling survival (Gordon and others 1989)

T6-State A1 to A2: Same as T1

T7-State A2 to A1: Same as T2

T8-State A2 to A3: Same as T3

T9-State A3 to A1 or A2: Same as T4

T10-State A to State C (Type conversion from woodland to grassland): Use of mechanical and chemical tree and shrub control and prescribed burning remove all trees and shrubs resulting in a conversion from woodland to annual grassland. In some cases, this transition may be irreversible without artificial regeneration of native woody species, especially if frequent fires and grazing suppress seedlings of woody species. Seeding and fertilization often accompanied tree and shrub control. At low-canopy covers, fire or natural mortality could remove woody species and conditions for resprouting or acorn germination and seedling establishment may be unfavorable.

T11-State C to State A: Recovery from grassland conversions may take decades or may be irreversible depending on the intensity and type of brush control practices. Repeated fires and grazing help to maintain the grassland. Blue oaks and other woody plants may colonize adjacent open grasslands but seedlings are seldom found more than 30 m from existing tree canopy.

T12-State C to State D: Planting, weed control, and protection of blue oak seedlings from animal damage can successfully restore blue oaks (McCreary 2001).

T13-State A to State E: Intense fire, wood cutting or vegetation management kills blue oaks and they do not resprout due to old age (Burns and Honkala 1990) or site conditions (DeLasaux and Pillsbury 1987; Haggerty 1991). Interior live oaks are top killed but resprout vigorously. With fire protection shrubs gradually increase producing a State similar to a but without blue oak.

T14-State A to F: Intense fire kills all trees and they do not regenerate (Haggerty 1991). Manzanita and/or Ceanothus reestablish from seed producing patches of shrubs mixed with open grassland.

T15-State F to A: On deeper soils with better moisture holding capacity interior live oak and/or blue oak regenerate from acorns that germinate under canopy of shrubs (Callaway and D’Antonio 1991; Muick 1997). This is a slow successional process.

Continue

Influence of Winter-Spring Livestock Grazing on Survival and Growth of *Quercus lobata* and *Q. agrifolia* Seedlings[1]

Claudia M. Tyler,[2] Bruce E. Mahall,[3] and Frank W. Davis [4]

Abstract

The relative importance of livestock grazing in limiting or enhancing oak recruitment remains unclear because results from previous studies have been contradictory. In Santa Barbara County, we have replicated large-scale planting experiments from 1997 to 2001 to determine the effects of cattle and other factors on seedling establishment of valley oak (*Quercus lobata*) and coast live oak (*Q. agrifolia*). We manipulated cattle grazing (ungrazed vs. winter-spring rotational grazing) and protection from small and large mammals. Rainfall and seed predation and herbivory by small mammals—most likely gophers and ground squirrels—significantly impacted rates of seedling recruitment. Exclusion of cattle alone has not significantly increased establishment of either valley or coast live oak. However, protected seedlings in pastures with cattle have higher survival and growth rates than protected seedlings in plots excluding cattle. Our results suggest that winter-spring livestock grazing can have indirect positive effects on oak establishment, by reducing herbaceous biomass and associated small mammals adjacent to protected seedlings. Contrary to expectations based on the relative abundance of natural oak seedling recruits, establishment and survival of coast live oak planted in our experiments has been significantly and consistently lower than that of valley oak.

Keywords: Cattle, coast live oak, mortality, oak recruitment, regeneration, sapling, valley oak.

Introduction

In a number of oak woodlands and savannas throughout the world, stands are composed of large, old adults with few individuals in the smaller, younger classes, raising concerns that natural recruitment of the oaks may be insufficient to balance adult mortality (Shaw 1968, Saxena and Singh 1984, Holzman 1993, Swiecki and others 1993, Loftis and McGee 1993, Russell and Fowler 1999). In California, these observations have stimulated many studies, which have demonstrated that oak seedling recruitment may be extremely limited in space and time as a result of many natural and anthropogenic factors operating independently or together (reviewed by Tyler and others 2006).

The role of cattle in affecting oak recruitment remains controversial. Cattle grazing has been implicated as being one of the main factors responsible for poor oak recruitment in rangelands. However, the relative importance of browsing by livestock vs. native herbivores such as deer in limiting natural oak recruitment remains unclear

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[1] An abbreviated version of the paper was presented at the Sixth California Oak Symposium: Today's Challenges, Tomorrow's Opportunities. October 9-12, 2006, Rohnert Park, California.

[2] University of California Santa Barbara, CA 93106. email: tyler@lifesci.ucsb.edu.

[3] University of California Santa Barbara, CA 93106. e-mail: mahall@lifesci.ucsb.edu.

[4] University of California Santa Barbara, CA 93106. e-mail: fd@bren.ucsb.edu.

and may be site- or region-specific (Muick and Bartolome 1987, Hall and others 1992, Standiford and others 1997, Swiecki and others 1997). This debate is complicated by the observation that the removal of livestock has rarely led to increased levels of oak recruitment, even after many decades (e.g., blue oaks, White 1966; valley oaks, Callaway 1992).

The Santa Barbara County Oak Restoration Program was funded as a long-term ecological study that would improve our understanding of the role of cattle and other factors in limiting or promoting establishment of oaks in large-scale, rangeland environments. Our previous findings (reported in Tyler and others 2002) indicate that rainfall, and seed predation and herbivory by small mammals—most likely gophers and ground squirrels—significantly impacted rates of seedling recruitment. This long-term program provides the opportunity to follow cohorts of seedlings as they transition to the sapling stage. Here, we describe survival and growth rates of *Quercus lobata* (valley oak) and *Q. agrifolia* (coast live oak) seedlings planted from 1997 to 2001, specifically evaluating the impacts of livestock grazing.

We chose to plant valley and coast live oak for several reasons. Valley oak was selected because it is the oak species of greatest concern in California, in large part because its reported recruitment is the lowest among all eight oak tree species in the state (Muick and Bartolome 1987, Bolsinger 1988, Barrett and Waddell this volume). This species has also been heavily impacted through various forms of development as its distribution coincides with areas of intense land use and land development, contributing to its perceived critical status. Coast live oak provides an excellent comparison to valley oak because it commonly occupies the same type of savanna and open woodland habitat, and it is reported to have much higher levels of natural seedling establishment. Of the three oak species dominant in Santa Barbara County, coast live oak has been the least studied.

Site Description

Research is being conducted on the Sedgwick Reserve, a 5,860-acre (2,372-ha) ranch managed by the University of California Natural Reserve System, and located at the base of Figueroa Mountain in the Santa Ynez Valley in central Santa Barbara County. The climate is Mediterranean, with hot dry summers and cool wet winters. Mean annual rainfall (calculated for a 55-year period) is 400 mm (15.8 inches). Total precipitation (as recorded at the nearest National Weather Service recording station) for the rain-years including 1996 to 2001, when acorn planting was conducted, ranged from 300 mm in 1996 to 1997 to 830 mm in 1997 to 1998.

Cattle grazing was managed by California Polytechnic State University, San Luis Obispo, from 1995 to 2002, and by Wise Acres Ranch from 2002 to 2006. Within our experimental areas (~525 acres), grazing paddocks range from 1 to 52 acres, with an average size of 23 acres. The timing and duration of grazing has varied from year to year, dependent on grass availability, but has been conducted each year in winter/spring between the period December and June. Herd size has also varied annually based on forage availability, but has averaged 124 heifers or cow/calf pairs.

Our experimental plots were 50 x 50 m. Fifteen of these large plots were controls, open to cattle grazing, and fifteen excluded cattle with the use of electric fence. The cattle exclosures were accessible to deer and pigs, which could go over or under the electric fence. In savanna areas, we centered each plot on an adult oak tree, the canopy of which covered an average of 10 percent of the total plot area. Eight plots were located in a treeless area that was clearcut in ~1950 (the "Airstrip"). Plots were paired, with one plot randomly selected to be fenced to exclude cattle. These plots were established in 1995.

Large-Scale Planting Experiments

We 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 (detailed methods described in Tyler and others 2002). In our large experimental plots, described above, we planted acorns collected from valley oak and coast live oak on the site. 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. The characteristics, or conditions, of these treatments varied depending on whether they were within large plots grazed by cattle or plots fenced to exclude cattle. Most notably, within grazed plots grass and herbaceous cover was reduced on average for all treatments, while ungrazed plots generally had abundant cover and biomass of grasses and other vegetation.

Large cages that protected from deer, pigs, and cattle within the plots were vertical cylinders 18" in diameter and constructed of 4' high, 2" x 4" mesh galvanized wire (12 gauge). Cages were supported at one side with a 5' t-post, and at the other side with a 4' rebar. This design was based on the "Vaca cage" described in Swiecki and Bernhardt (1991). Smaller cages to exclude both small and large mammals were vertical cylinders constructed of 3'-high hardware cloth (mesh size = 0.5"), sealed at both ends with aviary wire, and set 12" into the ground. Each treatment was replicated five times within each plot for each species, each planting year.

In winters of 1997, 1998, 2000, and 2001, we planted approximately 1,000 acorns of each species, two acorns per planting location. Number of locations planted per individual treatment (n) ranged from 65 to 180. Acorns and seedlings did not receive supplemental water.

Results and Discussion

Survival Rates

Seedling emergence and survivorship were both very low for acorns planted in 1997. Rainfall in 1996-1997 was well below average, with the last rainfall of the season occurring in mid-January 1997. Only 12 planting locations (1.2 percent of total planted) have 9-year-old seedlings (eight valley oak and four coast live oak locations). The treatment that was most successful was that which excluded small and large mammals. Only one open-planted valley oak seedling survived from the 1996-1997 cohort. There are more planting locations with seedlings present in areas that are grazed by cattle than in ungrazed areas (*table 1*).

Establishment was much higher in the subsequent planting years (1998, 2000, and 2001). Survival rates are above 50 percent overall for 8-year-old seedlings planted in 1998 and protected from small mammals (*table 1*). Planting success has varied greatly among years (most likely a function of rainfall), and the highest survival rates are for seedlings protected from small mammals. These two factors play the major role in affecting early seedling establishment (Tyler and others 2002), and therefore significantly impact long-term survival rates across treatments. Effects of livestock grazing appear to be more subtle.

Table 1*—Summary of current survival rates for valley oak and coast live oak seedlings planted 1997 to 2001 in plots grazed by cattle vs. those fenced to exclude cattle. Data are the percent of planting locations with a seedling (one or two) present in 2006. Asterisks indicate a significant difference between grazed and ungrazed plots for a given treatment (logit regression, P < .05).*

				GRAZED	UNGRAZED
	yr planted	sdling age	treatment	% survivorship	
Valley oak	1997	9 yr-old	open	1.3	0.0
			no lrg anim	2.7	2.2
			no sm or lg mammals	2.7	1.1
	1998	8 yr-old	open	4.7	5.6
			no lrg anim	16.4	7.0
			no sm or lg mammals	55.6	42.5
	2000	6 yr-old	open	1.5	3.8
			no lrg anim	4.6	8.8
			no sm or lg mammals	29.2	35.0
	2001	5 yr-old	open	1.5	2.5
			no lrg anim	0.0	2.5
			no sm or lg mammals	32.3	31.3
Coast live oak	1997	9 yr-old	open	0.0	0.0
			no lrg anim	1.3	0.0
			no sm or lg mammals	2.7	1.1
	1998	8 yr-old	open	0.0	0.0
			no lrg anim	**11.0***	***1.1**
			no sm or lg mammals	**53.4***	***25.8**
	2000	6 yr-old	open	0.0	0.0
			no lrg anim	1.5	0.0
			no sm or lg mammals	6.2	6.3
	2001	5 yr-old	open	0.0	0.0
			no lrg anim	0.0	0.0
			no sm or lg mammals	12.3	15.0

Comparing seedling survival in similar treatments planted in grazed plots to those in plots excluding cattle, allows one to examine both direct and indirect effects of livestock grazing. First, we can ask whether exclusion of cattle alone allowed for significantly higher survival. Comparing open treatments for both species and all years, establishment rates do not vary significantly between grazed and ungrazed plots. There were no significant differences, indicating that even if acorns are planted, removal of livestock grazing alone does not enhance oak establishment. Our findings also indicate that winter-spring livestock grazing alone is not a management tool that will promote natural oak recruitment in rangelands similar to those studied.

Competition with non-native annual grasses has been hypothesized to be a cause of low-recruitment rates in oaks (Griffin 1971, Danielsen 1990, Gordon and Rice 1993, Gordon and Rice 2000). Thus, livestock grazing may indirectly enhance oak seedling establishment by reducing competition. To isolate this indirect effect of grazing, one may compare the difference between survival of seedlings that are protected from both small and large mammals in grazed vs. ungrazed plots. This difference was significant only for the 1998 cohort of coast live oak (logit regression, $P < 0.001$), where survival of protected seedlings was higher in grazed areas.

Another potential indirect effect of cattle grazing and removal of biomass is change in small-mammal activity. For example, gopher activity has been found to be greater in ungrazed areas compared to grazed areas (Stromberg and Griffin 1996). Comparing the survival of seedlings planted in 1998 (the cohort experiencing effects of grazing removal the longest) and protected from large mammals only in grazed vs. ungrazed areas, rates were higher for those in grazed areas—significantly so for coast live oak (logit regression, $P = .026$) and nearly so for valley oak (logit regression, $P = .060$). Since small mammals have access to this treatment in both locations, this difference suggests that small mammal activity is greater in the ungrazed areas, and that livestock grazing may provide an indirect positive effect by reducing deleterious impacts of small mammals on oak seedling survival.

Contrary to our expectations, survival rates have been lower for coast live oak than for valley oak nearly every year, in every treatment. This result suggests that observed patterns of high natural recruitment in coast live oak (e.g., Bolsinger 1988, Barrett and Waddell this volume), are not due to higher seedling survivorship rates in this species, but may be a result of other factors, such as differences in acorn production or seed predation rates.

Seedling Growth

Heights of surviving seedlings vary among species and cohorts (*table 2*). As expected, on average, heights are greatest for the older cohorts, though the tallest individuals are those planted in 1998, an El Niño year with plentiful rainfall. Coast live oaks are slightly taller than valley oaks at the same age and in comparable treatments.

Table 2—*Growth of valley oak and coast live oak seedlings planted 1997 to 2001 in plots grazed by cattle vs. those fenced to exclude cattle. Data are mean seedling heights (cm) plus one standard error, for four seedling cohorts measured in July 2006. Asterisks indicate a significant difference between grazed and ungrazed plots for a given treatment (t-test, P < .05).*

				GRAZED	UNGRAZED
	yr planted	sdling age	treatment	mean ht in cm (& SE)	
Valley oak	1997	9 yr-old	open	8.0 (0)	-
			no lrg anim	105.5 (13.5)	81.5 (2.5)
			no sm or lg mammals	127.0 (67.0)	74.0 (0)
	1998	8 yr-old	open	19.1 (6.8)	32.1 (2.3)
			no lrg anim	71.2 (11.3)	60.8 (8.8)
			no sm or lg mammals	88.2 (6.2)	97.5 (9.5)
	2000	6 yr-old	open	11.0 (0)	15.7 (5.4)
			no lrg anim	**61.3 (5.2) ****	**** 38.6 (6.1)**
			no sm or lg mammals	63.5 (4.1)	59.0 (5.1)
	2001	5 yr-old	open	16.0 (0)	25.5 (12.5)
			no lrg anim	-	37.5 (2.5)
			no sm or lg mammals	53.1 (4.9)	45.9 (3.3)
Coast live oak	1997	9 yr-old	open	-	-
			no lrg anim	187.0 (0)	-
			no sm or lg mammals	140.5 (38.0)	159.0 (0)
	1998	8 yr-old	open	-	-
			no lrg anim	131.3 (31.4)	67.0 (0)
			no sm or lg mammals	130.5 (8.6)	138.8 (12.5)
	2000	6 yr-old	open	-	-
			no lrg anim	84.0 (0)	-
			no sm or lg mammals	68.0 (12.2)	84.2 (15.8)
	2001	5 yr-old	open	-	-
			no lrg anim	-	-
			no sm or lg mammals	63.4 (5.6)	58.5 (4.9)

Assessing the effects of livestock grazing, as above, on seedling height, we first compared open treatments in grazed vs. ungrazed areas, and found no significant differences (t-tests, P > .05), indicating that removal of cattle alone does not improve oak seedling growth. Examining indirect effects of grazing, we found no significant differences in the heights of seedlings protected from both small and large mammals in grazed vs. ungrazed areas, suggesting that removal of herbaceous biomass alone did not enhance growth rates of seedlings in grazed pastures. We did find evidence of a positive indirect effect of grazing on valley oak, related to small mammal effects. In our 2000 cohort, the seedlings protected from large mammals were taller in the grazed areas compared to the ungrazed areas (t-test, P = 0.026). As above, since small mammals have access to this treatment in both areas, this suggests that small mammal activity may have been greater in the ungrazed plots, thus reducing oak seedling growth.

Summary and Implications for Oak Restoration in Rangelands

Our experimental results suggest that several factors, especially rainfall and seed predation and herbivory by small mammals, play a significant role in limiting or promoting seedling recruitment of oaks. Excluding cattle has not enhanced survival or growth rates of planted unprotected valley or coast live oak seedlings. At the same time, cattle grazing by itself (without additional protection of seedlings) has not led to higher levels of oak establishment, as has been suggested by some range managers. These results indicate that winter-spring livestock grazing is unlikely to be solely responsible for low oak recruitment rates in California, nor is it the management tool that by itself will solve the “oak regeneration problem.” However, we found that indirect effects of grazing (on protected seedlings) were positive or neutral for survivorship and growth. These findings are similar to those reported for valley oak by Swiecki and Berhardt (1991). This result may not hold at higher stocking densities or if grazing is continued into the summer months when seedlings are more likely to be browsed.

The results of these experiments provide some guidance for those planting oaks in similar xeric rangeland settings by indicating the range of survival and growth one might expect if acorns are planted using these treatments. Swiecki and Bernhardt (1991) provide similar and very helpful guidelines for valley oak in Northern California. As discussed previously, survival and growth rates have varied considerably among years, planting cohorts, and species. Less variability could be expected if irrigation were used, though such methods are unlikely to be cost-effective in large-scale rangeland settings.

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Continue

Belowground Processes

Continue

Using ^{13}C and ^{15}N Isotopes to Study Allocation Patterns in Oak Seedlings [1]

Laura M. Suz,[2] María V. Albarracín,[3] and Caroline S. Bledsoe[3]

Abstract

In California's oak woodlands, survival and growth of oaks may depend on a symbiosis between oak roots and fungi that form ectomycorrhizas. Ectomycorrhizal (ECM) fungi are major players in carbon (C) and nitrogen (N) utilization and cycling because they facilitate water and nutrient uptake from the soil into the plant. The ECM fungi also benefit because plants supply carbohydrates to their fungal partners. Little is known about the stoichiometry of N and C exchange within ECM plants. It is not known whether N uptake and transfer from ECM fungi to their plant host is related to C flow from host to ECM fungi.

We considered several questions. Do plants "reward" those ECM fungal species that supply more N to the plant by providing more C to these ECM species? Are N and C transfers linked? Are ECM roots that take up more N from soils greater sinks for C? What are the long-term and short-term transfers of N and C, as measured by natural abundance (long-term) and tracer studies (short-term)? The natural abundance (background levels) of ^{15}N and ^{13}C in oak seedlings sheds light on what are the N sources for oaks, and how oaks allocate C over the long term (years to decades). Tracer data shed light on short-term processes of N and C allocation in oaks.

In this study, we explored these questions by tracking C and N transfers within ECM blue oak seedlings of *Quercus douglasii* Hook&Arn. First, we determined the natural abundance (background) of N and C in control seedlings. N natural abundance was higher in ECM roots than in other tissues, while C natural abundance was higher in leaves than in other tissues. We traced C transfer from oak shoots into oak ECM roots, as well as N transfer from soil into oak ECM roots and into oak shoots. Our results suggest that both leaves and ECM tips were strong sinks for C and N. The stoichiometry of N and C into and out of ECM roots can help us understand how ECM fungi affect C allocation within oaks and how oaks respond to N supply from ECM roots.

Keywords: Blue oak, carbon allocation, nitrogen uptake, stable isotopes, stoichiometry.

Introduction

Blue oak (*Quercus douglasii* Hook&Arn.) is a broadly distributed tree species in California and occupies about 40 percent of California oak woodlands (Adams and others 1997). It is thought that oaks are highly dependent on ectomycorrhizal (ECM) fungi for growth and survival since ECM fungi play important roles by providing water and nutrients for the host plant, while the host provides photosynthates to its symbiotic partner. Our current understanding of this relationship suggests that in all types of mycorrhizal associations, except for those involving orchids or

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[2] PhD student. Centre Tecnològic Forestal de Catalunya, Solsona, Spain ES-25280. e-mail: laura.martinez@ctfc.es.

[3] PhD student and professor, respectively, Department of Land, Air, and Water Resources, University of California, Davis, CA 95616. e-mail: mvalbarracin@ucdavis.edu; csbledsoe@ucdavis.edu.

mycoheterotrophs, the C requirements of the symbiosis are met by transfer of photosynthates from the plant to the mycorrhizal fungi within plant roots (Smith and Read 1997).

The cost of maintaining the symbiosis has been estimated to range between 10 and 30 percent of photosynthate (carbohydrate) production. Thus, mycorrhizas may act as strong sinks for plant photosynthates, stimulating host photosynthetic rates, improving host nutrition, and influencing nutrient transfer from the soil. Mycorrhizas constitute checkpoints for exchange of N and C at the plant-soil interface (Martin and others 2001). However we do not understand how ECM fungi affect C and N dynamics. For example, do plants “reward” certain ECM fungi that take up more soil N by supplying these ECM roots with more C than other ECM fungi that take up less soil N? Are C and N transfers into ECM roots linked?

Nitrogen is often the limiting nutrient for forest growth. Thus, N cycling has been extensively studied in forest soils. Plants cannot directly access atmospheric N_2 and rely on soils for their N. Plants may compete with other soil organisms (bacteria, saprobic fungi, etc.) for soil N. In addition, soil N may be less available to plants when this element is in soil organic matter. ECM fungi are able to access soil N in inorganic forms (ammonium, nitrate) and also in organic forms, such as labile organic N, amino acids and proteins. Clearly, there are benefits to plants to support their ECM fungi, as well as benefits to the ECM fungi by associating with plant roots.

Movement of soil N is usually considered to be unidirectional, beginning in the soil, continuing to plant roots and finally to shoots (Marschner 1995). Carbon movement in the plant is controlled by gradients between production (source organs such as leaves) and consumption (sink organs such as non-green tissues). Thus, C movement can be either bidirectional (translocation within the plant) or unidirectional (from shoots to stems, to roots and then into the rhizosphere soil).

The use of stable isotopes is a powerful approach to assess C and N interactions, especially belowground (Maillard and others 1994). Stable isotopes are a useful tool for analyzing the function of ECM fungi because variations in natural abundance of C and N, in both the plant host and the ECM fungi, may reflect the longer-term history of resource acquisition, loss, and internal cycling (Handley and Scrimgeour 1997). Ecological studies often use stable isotope data either at naturally occurring levels (natural abundance) or at levels outside the natural range (enrichment experiments). This enrichment technique involves an enrichment of the heavier isotope over background making the measurement of isotopic effects easy to detect, since the difference between natural abundance *vs.* enrichment is large. Moreover, variations in background natural abundance levels of most isotopes are very small, and stable isotope composition is usually reported as parts per thousand (‰). Changes in isotopic distributions of N and C across the fungal-host continuum can provide insights into the role of ECM fungi in N and C cycles.

Measurement of natural abundance of ^{13}C and ^{15}N isotopes in blue oak-ECM systems can give us a long-term (months to years and decades) view of C and N transfer into and out of both symbionts. In contrast, enrichment measurements give us a short-term view (hours to days), permitting us to follow the flows and rates of ^{13}C and ^{15}N without altering their natural behavior (Nadelhoffer and Fry, 1994).

In this study we asked four questions: First, what are the relative background (natural abundance) levels of the stable isotopes of C and N in different parts of blue oak seedlings? Second, how long does it take for foliar-applied C to move into roots and for soil-applied N to move into the plant? Third, will both C and N accumulate in fine and ECM roots? Fourth, are ECM roots stronger sinks for both C and N than other plant parts? These questions were investigated in a greenhouse experiment that measured transfers of the stable isotopes ^{15}N and ^{13}C in blue oak seedlings, applying ^{15}N to the soil and ^{13}C to the foliage.

Materials and Methods

Site Description and Experimental Design

Blue oak seedlings used in this greenhouse experiment were selected from a plot located within an oak-pine woodland at the University of California Sierra Field Research and Extension Center (SFREC) near Browns Valley, in northeastern California. SFREC is located in the Sierra Nevada foothills and has a typical Mediterranean climate. The plot was within an ungrazed site in the Koch Natural area (elevation ~600 m). Soils are classified as fine, mixed thermic Typic Haploxeralfs (Dahlgren and others 1997). Blue oaks are the dominant tree species; leaves emerge in late March; leaf drop usually occurs in October or November. The plot contained seedlings planted within nylon mesh cylinders to facilitate future removal of seedlings with intact roots. Seedlings were planted in 2002 and became mycorrhizal with ECM fungi native to the oak-pine woodland.

The greenhouse experiment included three treatments and four replicate seedlings for a total of 12 seedlings. Treatments were: (1) control (no ^{13}C or ^{15}N addition), (2) ^{13}C-glucose and ^{15}N-ammonium chloride (^{15}N-NH_4Cl) addition, and (3) ^{13}C-sodium bicarbonate (^{13}C-$NaHCO_3$) and ^{15}N-NH_4Cl addition. We chose glucose as a C source because it is rapidly transferred within the plant, although its absorption through leaves may be slow. We chose bicarbonate as a C source because it can be rapidly photosynthesized, although some CO_2 may be lost. Both ^{13}C treatments received ^{15}N-NH_4Cl application to the soil. We chose ammonium as a N source, since it does not leach from soils and would remain in the soil in the pots.

In March 2006, we dug up 12 blue oak seedlings within their mesh cylinders from our field plot, and we transferred the 4-year-old seedlings and associated soil into pots (10 cm x 10 cm x 30 cm). Seedlings had just begun to leaf out and had a few small leaves. Seedlings were allowed to acclimate to greenhouse conditions for two weeks while more seedling leaves emerged and expanded.

^{15}N and ^{13}C Labeling

Two weeks after seedlings were transplanted into pots, we added ^{15}N-NH_4Cl solution (27.5%N, 99 atom% ^{15}N) to the soil in all pots except the controls. In each of these pots, we injected 30 ml of isotopically enriched NH_4Cl solution in six locations around the seedling. We used an auto-refilling 18–gauge, 30 cm long syringe. The solution was released slowly as the needle was raised from the bottom to the top level of the pot over a distance of 25 cm. The amount of N injected into each pot was calculated to produce an average concentration of 2 μg N g^{-1} soil.

After two additional weeks in which seedlings continued to grow and acquire ^{15}N from the soil, we added ^{13}C to five leaves on each plant, not including the four control plants. We applied ^{13}C as either sodium bicarbonate or as glucose. The four seedlings in Treatment 2 received 8 ml/seedling of ^{13}C-labeled glucose (20mM, 40%C, 99 atom% ^{13}C). The four seedlings in Treatment 3 received 8 ml of ^{13}C-labeled $NaHCO_3$ (1mM, 15.3%C, 99 atom% ^{13}C). Labeled solutions in 2 ml-microcentrifuge tubes were attached to the leaves (five tubes, one/leaf). Each leaf was inserted into a microcentrifuge tube containing 1.6 ml of the ^{13}C-solution. We cut the end of each leaf to facilitate the absorption of the solution.

Tubes were attached to leaves on different branches, where possible, to create more uniform transfer into the entire plant. Tubes were attached vertically to branches and sealed with a small plug of glass wool to reduce evaporation. After three to four days, we re-filled the tubes with distilled water to enhance uptake of any remaining solution in the bottom of the tubes. During the day, seedlings were exposed to artificial light to increase absorption of ^{13}C-labeled solution. Plants were irrigated as needed, about once a week.

Harvest

In a sequential sampling with minimal disturbance to the soil, we removed a few ECM fine roots at four times: (1) before addition of the ^{15}N, day 0; (2) immediately before the addition of the ^{13}C, day 14; (3) the day after the addition of the ^{13}C, day 15; and (4) day 18. After 26 days, we harvested all plants, both roots and shoots. At each sampling time, except day 0, we collected three fine-ECM root samples from the upper root system (0-12 cm) and three samples from the lower root system (12-24 cm). These collections were done by opening the side of the plastic pot and carefully sampling several fine and ECM roots with minimal disturbance to the remaining roots and soil. Twelve days after application of ^{13}C (day 26), the tubes were removed and seedlings were harvested. We separated the plants into leaves, branches, stem and roots. Roots were further subdivided into four categories: taproot, coarse roots (> 2mm diameter), fine roots (0.5 < diameter > 2mm) and ECM roots (< 0.5mm diameter, bearing mycorrhizal tips). Height, stem diameter of the oaks and number of branches and leaves were recorded. Leaves to which tubes with ^{13}C-solutions were attached were not included in the isotopic analyses.

All plant materials were oven-dried (60°C, one week), weighed, ground to a fine powder and analyzed for total N, ^{15}N, total C and ^{13}C by a mass spectrophotometer at the University of California, Davis, Stable Isotope Facility. The four control seedlings, used to determine natural abundance of ^{15}N and ^{13}C, were harvested and analyzed similarly.

Calculations and Statistical Analyses

Two sets of samples were processed for isotope analyses, control seedlings for natural abundance determinations, and labeled seedlings for ^{15}N and ^{13}C enrichment. For natural abundance determinations, we harvested ECM root samples at day 0 and at day 26. For seedlings that received both ^{15}N and ^{13}C, we harvested fine ECM roots over time (day 14, 15, 18, and 26). This allowed us to determine the rate of transfer of both ^{15}N and ^{13}C into different parts of the seedlings.

We calculated δ^{15}N (‰) as follows (Shearer and Kohl 1993):

$$\delta^{15}N = [(^{15}N/^{14}N\text{sample} - {}^{15}N/^{14}N\text{standard})/\ (^{15}N/^{14}N\text{standard})] * 1{,}000$$

Similar calculations were done for ^{13}C -enriched samples:

$$\delta^{13}C = [(^{13}C/^{12}C\text{sample} - {}^{13}C/^{12}C\text{standard})/\ (^{13}C/^{12}C\text{standard})] * 1{,}000$$

Values were calculated relative to the international standard Vienna Dee Belemnite for ^{13}C (R=0.0112372) and for atmospheric N_2 for ^{15}N (R=0.0036765). For each individual sample, ^{15}N and ^{13}C % recovery was calculated as:

$\%^{15}$N recovery = (amount ^{15}N excess sample/total ^{15}N added into one seedling pot)*100

$\%^{13}$C recovery = (amount ^{13}C excess sample/total ^{13}C added into one seedling pot)*100

Where:

Amount isotope excess = (amount isotope/unit of tissue weight)*(atom% enriched sample - atom% control).

Data were analyzed using one-way ANOVA (^{15}N and ^{13}C parameters as main factors) or two-way ANOVA when isotopic composition per plant-part was compared (SPSS, Inc., Chicago, IL). Separation of means was performed using a Fisher's protected LSD at the 0.05 significance level.

Results

Seedling Biomass and Percent N

Since there were no differences among treatments in seedling biomass and percent N, data were averaged (n=12, *table 1*). Average seedling height was 24 cm and there were 2-5 branches/seedling and 15-45 leaves/seedling. Mean stem diameter was 7 mm, the mean length of the taproot was 24 cm. Seedling shoot to root ratio was 0.36±0.02. All seedlings were ectomycorrhizal.

Table 1—*Characteristics of Quercus douglasii seedlings. Values are means (n= 12) with standard errors.*

Plant part	Biomass (g)	Biomass allocation (%)	%N	N allocation (%)
Leaves	0.85±0.1	6.3±0.2	2.07±0.09	31.0±1
Branches	0.62±0.1	4.6±0.5	0.86±0.02	12.9±0.5
Stem	2.04±0.3	15±1.4	0.73±0.03	11.0±0.3
Taproot	8.20±1.4	62±1.7	0.45±0.03	6.7±0.4
Coarse roots	0.90±0.2	5.5±2	0.66±0.02	9.3±0.6
Fine roots	0.31±0.07	2.3±0.4	0.9±0.02	13.5±0.3
Ectomycorrhizal roots	0.58±0.05	4.3±0.3	1.03±0.05	15.6±0.9
	Total, 13.50		Mean, 0.96	

Natural Abundance

In control seedlings, natural abundance of δ^{13}C and δ^{15}N was higher in ECM roots than in other plant parts ($p<0.0001$), except leaves that had the highest δ^{13}C values ($p<0.0001$). Branches and stems had the lowest δ^{13}C values and together with coarse roots, had the lowest δ^{15}N values (*table 2*).

Table 2—*Natural abundance of ^{15}N and ^{13}C in Quercus douglasii seedlings. Values are means of seedlings from Treatment 2 only (n=4) with standard errors of the mean. Within columns, different letters denote significant differences (p<0.05).*

Plant part	δ15N(‰)	δ13C(‰)
Leaves	-3.79±0.46 b	-27.38±0.20 c
Branches	-4.87±0.29 a	-28.63±0.27 a
Stem	-4.37±0.34 b	-28.89±0.33 a
Taproot	-3.14±0.33 b	-27.90±0.25 b
Coarse roots	-4.59±0.16 a	-27.82±0.26 b
Fine roots	-3.47±0.21 b	-28.05±0.20 b
Ectomycorrhizal roots	-0.69±0.16 c	-27.89±0.11 b

Recovery of ^{15}N and ^{13}C in the Seedlings

The ^{15}N moved rapidly from soil into the plants; percent recovery was 1.7 percent. About half of the ^{15}N remained in the roots, half moved above ground, primarily into leaves (*fig. 1a*). Very little ^{13}C from the bicarbonate source was taken up by oak seedlings, thus, bicarbonate was not a satisfactory labeling method. However, in ^{13}C-glucose treated seedlings, ^{13}C moved into all plant parts. The percent recovery was 0.18 percent of the ^{13}C applied to the leaves. About 76 percent of the ^{13}C in the plant remained in leaves and branches and about 24 percent moved to the roots (mainly fine and ECM-roots; *fig. 1b*).

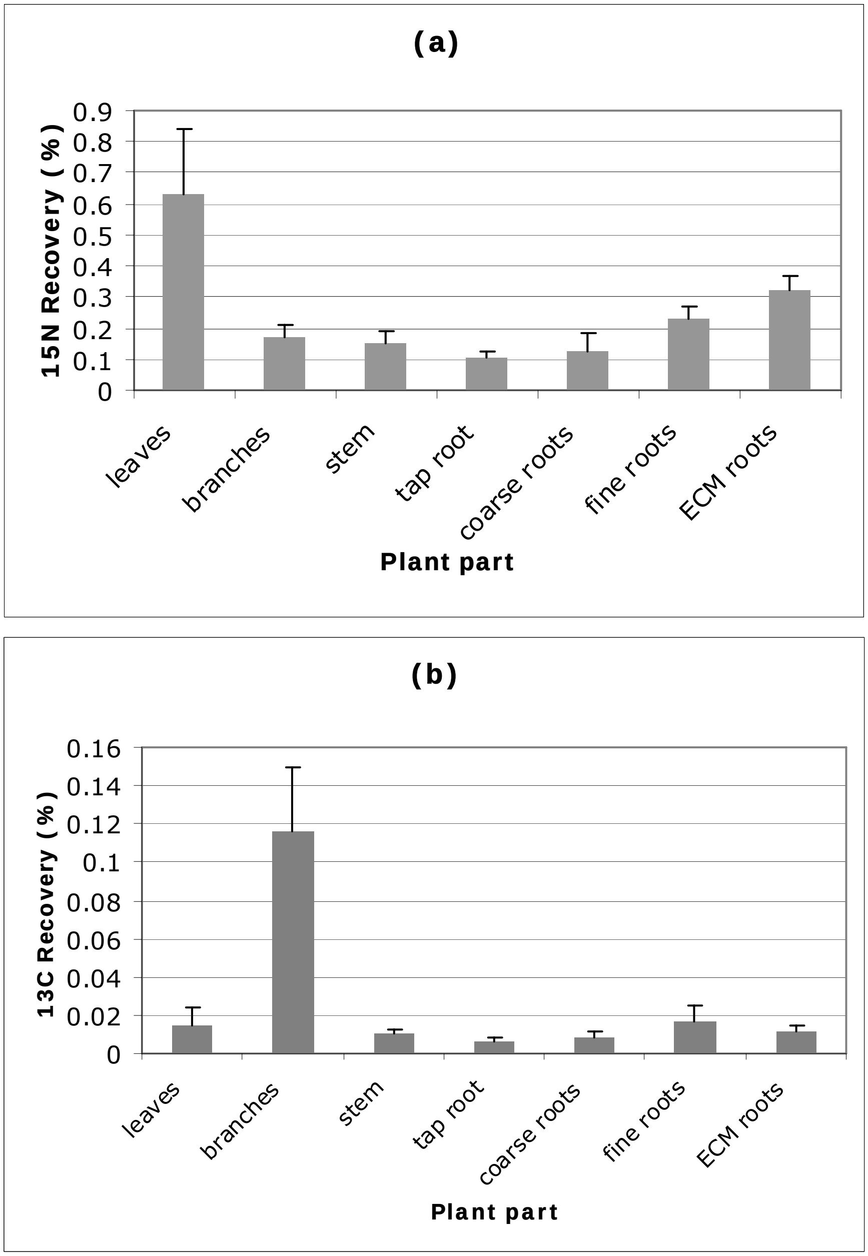


Figure 1—Percent recovery after 26 days: (a) ^{15}N and (b) ^{13}C. ^{15}N-ammonium was applied to the soil, ^{13}C-glucose was applied to oak leaves. Values are means from Treatment 2 seedlings (n = 4) with standard errors shown by vertical bars.

^{15}N and ^{13}C Uptake into Fine-ECM Roots Over Time

We found ^{15}N in the ECM and fine roots of seedlings within 14 days, at which point we applied ^{13}C-glucose to four seedlings and ^{13}C-bicarbonate to four seedlings. We sampled a few ECM roots from each seedling from day 0 (^{15}N addition) to day 14 (^{13}C source addition) and to days 15, 18, and 26 (final harvest). Values of δ^{15}N increased from 4 to 26 days after ^{15}N application (*fig. 2a*). We detected ^{13}C from the labeled glucose one day after application (day 15); δ^{13}C values continued to increase over time. We could not detect ^{13}C from sodium bicarbonate even 12 days after its application (day 26) (*fig. 2b*).

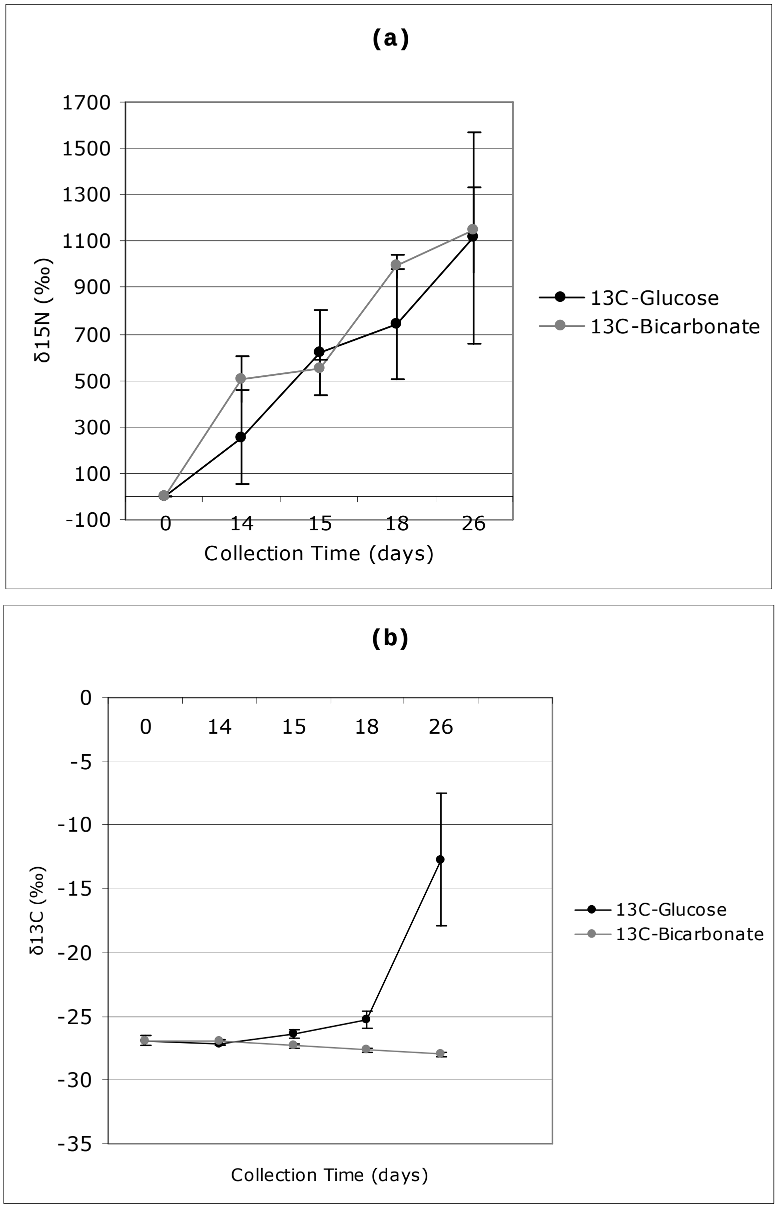
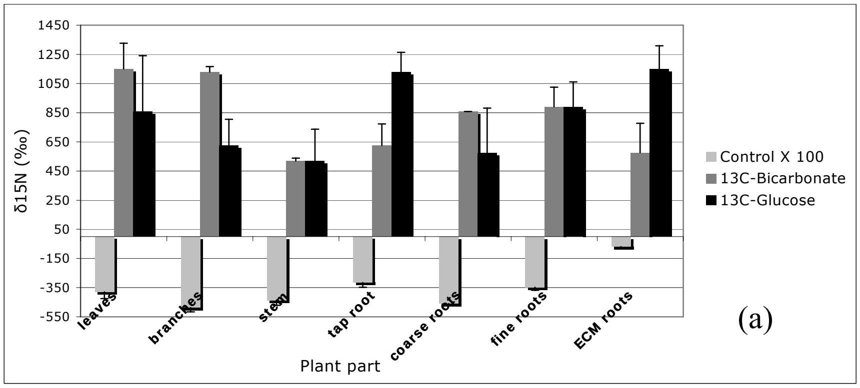


Figure 2—Transfer of ^{15}N and ^{13}C into fine-ECM blue oak seedling roots, 26 days after ^{15}N application to soil in day 0, and 12 days after ^{13}C application to leaves (day 26); (a) δ^{15}N (‰) and (b) δ^{13}C (‰). Values are means of Treatments 2 and 3 (n=4 for each) with standard errors of the mean shown by the vertical bars.

^{15}N and ^{13}C Allocation in the Seedlings

^{15}Nitrogen and ^{13}C from glucose were both readily detectable in all parts of the seedlings. Since we did not find differences in δ^{13}C and δ^{15}N values between the upper and the lower part of the oak roots, data were averaged. There were no significant differences in δ^{15}N in seedlings treated with either ^{13}C source (*fig. 3a*). Similarly, there were no significant differences in δ ^{13}C in control seedlings and seedlings treated with ^{13}C-bicarbonate (*fig. 3b*).



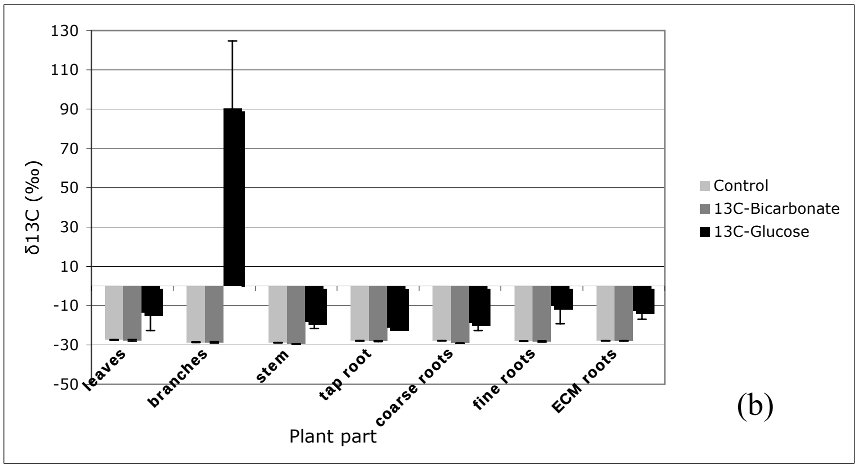


Figure 3—Allocation of ^{15}N and ^{13}C in oak seedlings after 26 days. (a) δ^{15}N (‰) and (b) δ^{13}C (‰). Light grey bars: control; dark grey bars: ^{13}C-bicarbonate treatment; black bars: ^{13}C-glucose treatment. Note: δ^{15}N values for control seedlings are multiplied by 100 for visibility.

Amount of ^{15}N and ^{13}C Transferred into Plant Parts

The greatest amount of ^{15}N was found in leaves (87 ng ^{15}N/mg dry weight) followed by ECM-roots (44 ng ^{15}N/mg dry weight) and fine roots (~32 ng ^{15}N /mg dry weight; *table* 3). Although much of the ^{13}C remained in the branches (54.5 µg ^{13}C/mg), some ^{13}C was transferred into fine and ECM roots.

Table 3—*Transfer of ^{15}N and ^{13}C within oak seedlings after foliar application of ^{13}C-glucose and soil application of ^{15}N-NH_4Cl. Values are means of Treatment 2 seedlings (n=4) with standard errors. Within columns, different letters denote significant differences ($p<0.05$).*

Plant part	^{15}N ng/mg tissue	^{13}C µg/mg tissue
Leaves	87.1±29.1a	6.70±4.7b
Branches	23.4±0.5b	54.5±15.7a
Stem	20.8±0.6b	4.70±1.4b
Taproot	14.6±0.3b	3.10±0.6b
Coarse root	17.0±0.8b	3.80±1.6b
Fine roots	31.8±0.5b	7.90±3.9b
Ectomycorrhizal roots	44.5±0.7b	5.50±1.2b

Discussion

Seedling Biomass and Percent N

The goal of this experiment was to follow transfer of the isotopes through the oak seedlings. Treatment with ^{15}N and ^{13}C did not affect seedling nutrient status, and control untreated seedlings did not differ in biomass and percent N from the seedlings treated with ^{15}N and ^{13}C. Leaves and fine and ECM roots were only 11 percent of the total plant biomass, but contained 60 percent of the total plant N. In contrast, the taproot represented 60 percent of the seedling biomass, but contained only 7 percent of the total plant N. We expected to find high amounts of N in fine and ECM roots since N assimilation in trees occurs almost entirely in root tips (Martin and Botton 1993). The high percent N in leaves might be due to the high N requirement for protein synthesis during production of foliage. In our experiment, foliar percent N was significantly greater than root percent N, as was shown for *Q. douglasii* by He and others (2006). In this study, the oak shoot-to-root ratios were similar to those reported for the same species by Cheng and Bledsoe (2005).

Natural Abundance

Natural abundance of stable isotopes presents a time-integrated long-term picture of functional processes that are usually difficult to measure directly (Robinson 2001). In contrast, enrichment studies present a short-term view of the movement and storage of these isotopes. In our experiment, natural abundance of both ^{15}N and ^{13}C isotopes was measured in control untreated seedlings. ECM roots from these control plants had higher $\delta^{15}N$ values than any other plant parts, indicating their active role in nitrogen uptake. Fungal $\delta^{15}N$ values increased with the proportion of N taken up and transferred to the plant, leading to a greater difference between fungus and host. The higher values of $\delta^{15}N$ in ECM roots are mainly due to fractionation against ^{15}N during the transfer of N from fungus to the host (Taylor and others 2003). The ^{15}N

abundance in plants is closely related with the presence and type of mycorrhizae (Michelsen and others 1998, Emmerton and others 2001). The sporocarps are enriched in ^{15}N compared to plants (Gebauer and Dietrich 1993, Taylor and others 1997, Hobbie and others 1999, Trudell and others 2004). Even the sheaths of ECM fungi are enriched, compared to their host plants (Högberg and others 1996).

Delta^{13}C values were higher in leaves, as expected, since leaves are actively photosynthesizing carbon into carbohydrates and thus, are a strong sink for C. Delta^{13}C values were also high in roots that were also a strong sink for C. Enrichment in ^{13}C by ECM roots could be due to demand by the fungi for ^{13}C-enriched carbohydrates (Henn and Chapela 2001). Further studies are in progress to determine if different ECM types (morphotypes or genetically different genera and species) are greater sinks for N and C than other species.

Recovery of ^{15}N and ^{13}C in the Seedlings

After 26 days, recovery of both ^{15}N and ^{13}C was low, suggesting that longer times might be required for the isotopes to move throughout the plant. There are other possible causes of low recovery. For example, low ^{15}N recovery might be due to slow root growth relative to shoot growth, since the young seedlings had rapidly expanding leaves. In addition, greenhouse conditions may increase nitrification processes, during which, isotope discrimination can be as great as a 40‰ of fractionation factor. ECM fungi generally prefer ammonium over nitrate as an N source. However, under limiting supplies of ammonium, nitrate (depleted after mineralization) would represent an alternative N source. Thus, seedlings could have taken up naturally occurring un-labeled nitrate instead of ammonium, leading to a low recovery of the ^{15}N. Recovery of ^{13}C was low, perhaps due to difficulties in absorption of the glucose by the somewhat thick cuticle on the oak leaves. Perhaps transplant shock in moving seedlings from the field to the greenhouse may have contributed to the low recovery.

We expected to find ^{13}C primarily in the unlabeled leaves, but were surprised to find 76 percent in the leaves, stem and branches, but mainly in the branches. We suspect that enrichment was lower in leaves, due to dilution effects from photosynthesis of unlabeled carbon dioxide. The incorporation of new unlabelled carbon ($^{12}CO_2$) from the atmosphere, used for photosynthesis in the leaves, would dilute the ^{13}C pool and decrease the $^{13}C/^{12}C$ ratios in the leaves. We suspect that much of the enrichment in the stems was due to incorporation of ^{13}C into structural materials (cellulose, etc.).

^{15}N and ^{13}C Uptake and Allocation

The ^{15}N from the NH_4Cl was detected in fine roots at our first sampling time, 14 days following its application into soil and continued to increase up to our final harvest at 26 days. Cheng and Bledsoe (2005) and He and others (2006) reported similar rapid transfer of ^{15}N in oak seedlings and saplings. Transfer of ^{15}N within the plant occurs from ECM roots to leaves. It is assumed that a fraction of the N taken up from the roots passes upwards in the xylem to the shoot, where it is transferred to the phloem. The remaining fraction is transferred directly to the root phloem (Dewar 1993). Leaves might act as N sinks since we recovered a significantly greater percentage of ^{15}N in leaves than in the rest of the plant.

We could not detect ^{13}C from the bicarbonate, indicating no or very low absorption of this ^{13}C source by the leaves. However, the movement of glucose-derived -^{13}C from the leaves to the fine and ECM roots was rapid; we detected ^{13}C one day after its application. Other authors have also reported similar rapid transfer of labeled-C to the roots (Taylor and others 2004). We detected high amounts of ^{13}C in the branches so they may act as storage organs of C.

Conclusions

In this study we asked four questions:

(1) What are the background (natural abundance) levels of the stable isotopes of C and N in the different parts of blue oak seedlings? – We found that ECM roots had significantly higher $\delta^{15}N$ values than other plant parts, while leaves had significantly higher $\delta^{13}C$ values. Branches and stems had the lowest $\delta^{13}C$ values and, together with coarse roots, had the lowest $\delta^{15}N$ values.

(2) How long does it take for foliar-applied C to move into roots and for soil-applied N to move into the plant? – We tested the suitability of ^{13}C-labeled glucose and bicarbonate as ^{13}C sources applied to the leaves of the seedlings. We found that bicarbonate was not suitable as a ^{13}C source applied into the leaves. However, feeding leaves with ^{13}C-glucose, under controlled conditions, was efficient for labeling above- and below-ground biomass of blue oak seedlings. We discovered that it takes one day for ^{13}C to get into the roots. It probably takes less than 14 days for the ^{15}N to get into the roots and less than 26 to get into the leaves. Translocation of N and C through the plant is fast, even when applying the ^{15}N in soil, where there are other organisms that utilize this element. It would be necessary to sample roots earlier than 14 days to know how rapidly N moves to the leaves.

(3) Will both C and N accumulate in fine and ECM roots? – Yes, N accumulated in fine and ECM-roots and C was found in fine and ECM roots in higher amounts per mg of tissue than in the taproot and coarse roots, although taproots are more directly linked to the C transfer pathway from leaves than are fine roots.

(4) Are ECM roots stronger sinks for both C and N than other plant parts? – Yes, ECM roots acted as strong sinks of C and N but both elements were translocated to other parts of the plants also. In addition to ECM roots, leaves were also strong sinks for C and N, probably due to demand for protein synthesis for leaf development.

In further studies, this tracer methodology combined with morphotyping and molecular identification of the ECM tips, might allow us to know the individual $\delta^{15}N$ and $\delta^{13}C$ values of each fungal species on plant roots. Using these values, we could determine which ECM species supply more N to their host plant. Species with higher $\delta^{15}N$ values may transport a greater proportion of their N to their plant host (Hobbie and others 1999). In response, the plant may reward the fungus and transfer more C to these fungal species. This information about C and N cycling in oak seedlings can be extended to California oak woodlands, and further research on this topic will provide information that could be implemented in designing more efficient management practices for oak ecosystem conservation.

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Continue

Oaks Belowground: Mycorrhizas, Truffles, and Small Mammals[1]

Jonathan Frank,[2] Seth Barry,[2] Joseph Madden,[2] and Darlene Southworth[2,3]

Abstract

Oaks depend on hidden diversity belowground. Oregon white oaks (*Quercus garryana*) form ectomycorrhizas with more than 40 species of fungi at a 25-ha site. Several of the most common oak mycorrhizal fungi form hypogeous fruiting bodies or truffles in the upper layer of mineral soil. We collected 18 species of truffles associated with Oregon white oak. Truffles do not release spores directly into the air, but remain closed belowground. In conifer ecosystems, animals eat truffles and disperse the spores, providing mycorrhizal inoculum for new roots. We did a survey to determine the extent that small mammals eat hypogeous fungi and defecate the spores, thus dispersing mycorrhizal inoculum. We trapped small mammals near Oregon white oaks and examined fecal pellets for hypogeous fungal spores. Three species of rodents, California voles (*Microtus californicus*), deer mice (*Peromyscus maniculatus*), and harvest mice (*Reithrodontomys megalotis*), had 12 species of fungal spores in their fecal pellets. The most common spores in fecal pellets were those of *Tuber candidum*/*T. quercicola*, *Hydnotryopsis setchellii*, and *Cazia flexiascus*, all Ascomycota. Seedlings growing in the root zone of mature oaks have access to the mycorrhizal network of parent trees, but seedlings germinating outside the root zone may lack mycorrhizal sources. If the mycorrhizal community on saplings located away from mature oaks includes hypogeous fungi, then small mammals may be dispersing fungal spores into shrublands where saplings are located. We examined roots of oak saplings at distances up to 72 m from mature oaks and found mycorrhizas of *Tuber candidum* and *Peziza infossa*, both hypogeous species, suggesting that small mammals disperse spores for mycorrhizal inoculum. We propose a model that identifies the major players in oak ecosystems and hypothesize that regeneration of oak woodlands depends on the dispersal of mycorrhizal fungal spores by small mammals.

Keywords: Hypogeous fungi, mycophagy saplings, mycorrhizal inoculum, Oregon white oak, Quercus garryana.

Introduction

Roots of oaks form mycorrhizas with fungi (Cairney and Chambers 1999). These are beneficial fungi, not related to sudden oak death. A mycorrhiza, literally a fungus root, is an oak root tip growing closely with a particular fungus (Agerer 1991, Smith and Read 1997). In ectomycorrhizas, fungal cells form a sheath or mantle around the root. Fungal hyphae penetrate between the outer cortical cells to form the Hartig net, a network of hyphae that exchange nutrients with the root cells. Also, hyphae emanate from the mantle outward into the soil where they take up water and nutrients, particularly nitrogen and phosphorus, and transfer these to the root. The tree provides carbon compounds to the fungi.

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[2] Department of Biology, Southern Oregon University, Ashland, OR 97520.

[3] To whom correspondence should be sent: southworth@sou.edu.

In the upper layers of soil, virtually every root tip of Oregon white oak (*Quercus garryana*) is covered with the mantle of a mycorrhizal fungus (Valentine and others 2004, Moser and others 2005). So this is not a casual occurrence, but a regular feature of oak root structure. Ectomycorrhizas are found on all oak species and other members of the beech family (beech, tanoak), as well as in a few other families, for example, the pine family and the birch family.

Oregon white oak forms ectomycorrhizas with more than 40 species of fungi at a 25-ha site (Valentine and others 2004). The identity of ectomycorrhizal fungi associated with roots is hinted at by collecting the fungal fruiting bodies under the oaks, but confirmation of the identity is determined by comparing DNA of mycorrhizas with that of fruiting bodies or with fungal DNA sequences in a public database, for example, GenBank (Gardes and Bruns 1993).

Several of the most common oak mycorrhizal fungi form hypogeous fruiting bodies or truffles (both Ascomycota and Basidiomycota) in the upper 10 to 20 cm of mineral soil. Truffles do not release spores directly into the air, but remain closed belowground (Castellano and others 2004). Spores are dispersed by mycophagists, animals that eat the fruiting body and disperse the spores by defecation. In pine and Douglas fir forests of California and the Pacific Northwest, hypogeous fungi are eaten by small mammals, for example, flying squirrels, red-backed voles, and chipmunks (Hayes and others 1986, Izzo and others 2005, Maser and others 1978, Meyer and others 2005, North and others 1997), that disperse spores in fecal pellets.

Ectomycorrhizas of oaks also form with epigeous fungi—mushrooms, puffballs, jelly fungi, and crust fungi (Valentine and others 2004, Avis and others 2003, Walker and others 2005). Epigeous fungi emerge above the leaf litter and release their spores into the air where they are dispersed by air currents.

Oregon white oak seedlings initially obtain mineral nutrients and carbon from the cotyledons of the acorn for development of the initial root, which consists largely of a long tap root. By spring of the first year, the leaves emerge providing photosynthetic tissue for a source of carbon; the roots form lateral branches. Roots of seedlings germinating from acorns that fall under parent trees would grow in the fungal network of the parent tree. Thus the network of mycorrhizal mycelia emanating from parent tree mycorrhizas could serve as a source of mycorrhizal inoculum for the tips of lateral roots.

However, not all acorns germinate under the parent tree. Some are carried away by animals, such as ground squirrels and scrub jays, that move acorns and cache or bury them. Some of the cached or buried acorns also germinate, but the roots of these seedlings may not reach the mycorrhizal network of mature trees in areas where there are no ectomycorrhizal plants.

There is the common perception that fungi are “everywhere,” and indeed some fungi are widespread. However, mycorrhizal fungi are not ubiquitous because they are obligate heterotrophs on green plant hosts—they must be attached to roots for food. Mycorrhizal fungi live where they can interact with tree roots, and not just any tree roots but those of appropriate host trees. In conifers, transfers of soil or of truffle spores enhanced mycorrhizal formation of seedlings (Amaranthus and Perry 1987; Castellano and Trappe 1985).

Our questions relate to dispersal of inoculum for oak seedlings. How do seedlings germinating outside the root zone of mature trees encounter fungi that can form mycorrhizas? If seedlings are successful, they grow into saplings. Do saplings, derived from successful seedlings, have mycorrhizas? Is the ectomycorrhizal community of saplings composed predominantly of epigeous fungi with airborne spores or does it include hypogeous fungi that would be dispersed by animals? Because so few seedlings survive beyond a few years, we chose to investigate the mycorrhizal communities of saplings, which are those seedlings that clearly have survived. This gives a longer-term view of mycorrhizal communities associated with survival.

The answers to these questions will influence our understanding of the elements required for natural regeneration in an oak woodland ecosystem. In addition, we could define important components of restoration practices where acorns or oak seedlings are planted to restore oak woodlands.

Methods

We collected truffles, trapped small mammals, and sampled sapling roots of Oregon white oak (Garry oak, *Quercus garryana*) at Whetstone Savanna Preserve (42˚25'N, 122˚54'W) north of Medford, Oregon, at an elevation of 400 m. Shrublands of buck brush (*Ceanothus cuneatus*) surround the oaks (Valentine and others 2004). No other ectomycorrhizal shrubs or trees were present.

We found truffles by raking under and around Oregon white oaks and examining the leaf litter and loose soil. Fungi were identified by use of keys and descriptions (Gilkey 1916, 1954; Trappe 1979, 1989; Arora 1986; Castellano and others 1989; Trappe and Castellano 1991; Hansen 2001; Fogel and States 2002, 2003; Frank and others 2006a, 2006b, 2006c). Preliminary fieldwork showed that spring (April to June) was the primary fruiting season for truffles under Oregon white oaks in this climatic region (Frank and others 2006).

For small mammal trapping, 60 Sherman live traps were set in a 10-m grid around Oregon white oaks and in the surrounding buck brush in spring 2003 and 2004 (Frank 2005, Frank and others 2006). In spring 2006, 80 traps were set at 10-m intervals up to 50 m from the trunks of Oregon white oaks. Trapped animals were identified and released; fecal pellets were stored at 4^{o} C.

For spore identification, slides of fresh fecal pellets were stained with Melzer's reagent and viewed with a compound microscope. Spores were identified, based on comparisons to sporocarps collected at the research site and to descriptions in Castellano and others (1989) and in consultation with J. M. Trappe at Oregon State University.

Mycorrhizal oak roots were obtained from soil samples collected under saplings of Oregon white oak. Saplings, 0.7 to 4.5 m in height at distances of 3.4 to 72.0 m from mature trees, were sampled April to June 2004. Soil samples were rinsed through sieves with 0.59 and 0.15 mm openings (Moser and others 2005). Mycorrhizas were grouped by morphotype (Agerer 1991, Goodman and others 1996, Valentine and others 2004).

Results

Eighteen species of truffles were collected over two years *(table 1)*. Most were Ascomycota; five (*Gymnomyces* sp., *Hymenogaster boozeri*, *Melanogaster euryspermus*, *Scleroderma cepa*, and *Zelleromyces gardneri*) were Basidiomycota.

Spores from 12 taxa were found in fecal pellets of small mammals. California voles ate the greatest diversity of species, followed by deer mice and harvest mice *(table 1)*.

The ectomycorrhizal community on sapling roots included *Tuber* species, *Peziza infossa,* and *Scleroderma* sp. *(table 1)*. These were the most abundant hypogeous fruiting bodies under mature Oregon white oaks at this site. Epigeous fungi were also present on sapling roots. All sapling root tips were mycorrhizal.

Table 1—*Truffle fruiting bodies collected at Whetstone Savanna Preserve in southern Oregon; truffle spores in fecal pellets of 10 California voles,* Microtus californicus *(M); 10 deer mice,* Peromyscus maniculatus *(PE); and 8 harvest mice,* Reithrodontomys megalotis *(RE); and truffle fungi as mycorrhizas on roots of Oregon white oak saplings. Fruiting bodies were collected and rodents trapped near Oregon white oaks at Whetstone Savanna Preserve in southern Oregon, USA, in 2003 and 2004.*

	Small mammal			
Fungus	**MI**	**PE**	**RE**	**Sapling**
Balsamia alba	0	0	0	0
Cazia flexiascus	+	+	+	0
Genabea cerebriformis	+	+	0	0
Genea gardneri	0	0	0	0
Genea harknessii	+	0	0	0
Gymnomyces sp	+	+	+	0
Hydnotryopsis setchellii	+	+	0	0
Hymenogaster boozeri	+	0	0	0
Melanogaster euryspermus	0	0	0	0
Pachyphloeus citrinus	+	+	0	0
Pachyphloeus austro-oregonensis	+	+	0	0
Peziza ellipsospora	+	+	0	0
Peziza infossa	+	+	0	+
Scleroderma cepa	0	0	0	+
Tuber candidum/T. quercicola	+	0	+	+
Tuber whetstonense	0	+	0	+
Zelleromyces gardneri	0	0	0	0

Rodents did not remain particularly close to trees. In 2006, rodents were trapped at 40 m from trees with the greatest number trapped at 30 m from trees *(table 2)*. Saplings also occurred in this range with 87 percent of saplings within 40 m of mature trees.

Table 2—*Rodents trapped at distances from mature Oregon white oaks at Whetstone Savanna Preserve in southern Oregon in 2006. MI,* Microtus californicus; *PE,* Peromyscus maniculatus *RE,* Reithrodontomys megalotis.

Distance (m)	**MI**	**PE**	**RE**	**Total**
10	1	1	0	2
20	1	6	1	8
30	14	8	2	24
40	11	6	0	17

Discussion

Our data show that the ectomycorrhizal communities of saplings of Oregon white oak, growing outside the root zone of mature trees, include both epigeous and hypogeous fungal species. The presence of hypogeous fungi on sapling roots suggests that animal vectors disperse truffle spores from mature trees, where the fruiting bodies occur, out into shrublands, where saplings occur. Truffle spores were found in the fecal pellets of small mammals, and these animals were trapped in shrublands where saplings grow. The correlation of presence of spores in rodent fecal pellets with the general forming ectomycorrhizas on saplings distant from parent trees suggests a causal link in the dispersal of mycorrhizal inoculum by small mammals.

Truffles with hypogeous fruiting bodies have evolved under selection pressure for survival in warm dry climates (Castellano and others 2004). In such Mediterranean climates with seasonal drought, hypogeous fungi may be important survival elements for oak ecosystems. They provide food for small mammals in the spring when seeds are scarce. In addition, in the spring, oak seedlings that germinated in winter and formed a tap root, develop fine roots that become mycorrhizal.

We propose a model for natural regeneration of oaks (figure 1). In autumn, some acorns are dispersed by animals away from the parent trees. Some are cached in shrublands and not all are eaten. Acorns of Oregon white oak germinate in winter, producing a long tap root. In spring, lateral roots develop. At this time, truffles produce fruiting bodies in the upper soil layers around mature oaks. Small mammals eat them and move into the shrublands. Spores in fecal pellets, as well as airborne spores of epigeous fungi, form mycorrhizas with the young lateral root tips. These mycorrhiza are likely critical for their survival. The regeneration of oaks out from under mature trees may require two animal vectors—one for acorns in autumn and one for truffle spores in spring. We recognize that this model is largely hypothetical and needs further research for verification.

Currently, we are testing the hypotheses that mycorrhizal inoculum declines as a function of distance from mature oaks and that the mycorrhizal community on first-year seedlings outside the root zone of mature trees is composed of the fungi found as spores in rodent fecal pellets.

If our model is correct, natural regeneration of oaks would require fungi and small mammals as part of a healthy ecosystem. Restoration practices for oaks, in which people serve as the vectors for acorn dispersal, would also require inoculum dispersal—either as fungal spores or as mycorrhizal fungal hyphae in soil from under mature trees.

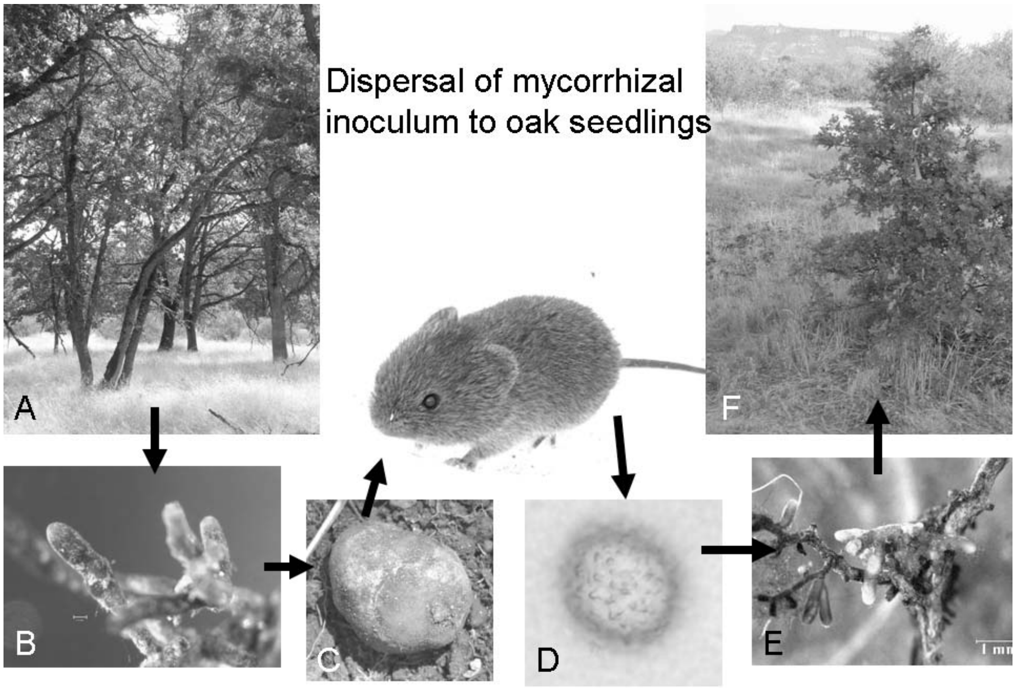

Figure 1—Model of dispersal of mycorrhizal inoculum to oak seedlings. Oregon white oaks (A) form mycorrhizas on virtually every root tip (B). Mycorrhizal fungi produce fruiting bodies seasonally (C). Hypogeous ones (truffles) (C) are eaten by rodents such as the California vole (D) that disperse truffle spores via fecal pellets (D). Truffles form mycorrhizas with seedling roots (E) that develop into saplings (G).

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Continue

Evaluation of Two Techniques for Quantification of Hyphal Biomass[1]

Meagan M. Hynes,[2] Robert J. Zasoski,[2] and Caroline S. Bledsoe[2]

Abstract

Currently, oak woodlands of Northern California and their associated mycorrhizal fungi are receiving more attention. In order to address the impact mycorrhizal fungal associations have on survival of various tree species in oak woodlands, we investigated the extramatrical fungal hyphae associated with several mature oak woodland tree species. Specifically our objective was to quantify the fungal hyphal biomass in soils near blue oak (*Quercus douglasii*), interior live oak (*Quercus wislizeni*), foothill pine (*Pinus sabiniana*), and Ponderosa pine (*Pinus ponderosa*). We developed methods to determine hyphal length using microscope images with either WinRHIZO Pro 2002©[3] software or the more common gridline intersect method (GIM), which calculates hyphal length using Newman's original (1966) and modified equations (Tennant 1975). After comparing methods, we found that using microscope images in addition to Tennant's equation resulted in the most accurate and efficient way of estimating hyphal biomass. Information gathered will be used to determine whether hyphal length is correlated with survival and growth of oaks in California's oak woodlands.

Keywords: Blue oak, extramatrical hyphae, foothill pine, hyphal length, interior live oak, ponderosa pine.

Introduction

Oak woodland regeneration has received considerable attention from managers during the last three decades. Low survival rates of blue oak saplings were investigated by Bernhardt and Swiecki (2001), yet no effective mitigation strategy exists to increase natural regeneration and survival rates. One possible explanation that has not been explored is the effect of mycorrhizal fungi and hyphae have on survival of oak woodland tree species. The symbiotic relationship between trees and mycorrhizal fungi has been shown to aid in nutrient and water uptake, and to protect roots from pathogens (Read and Leake 1989, Sylvia 1999, Wollum 1999). However, the effect of mycorrhizal associations on oak woodland tree species has not been explored as a possible solution to increase sapling survival rates. Moreover, there are few studies that have harvested and quantified fungal hyphae in the California oak woodlands.

Extramatrical fungal hyphae are the web-like structures that emanate from the plant root-fungal interface into the surrounding soil. Due to their extensive surface area, hyphae can increase access to nutrient and water uptake in the soil (Van Der Heijden and Sanders 2003). However, examining the proliferation and function of

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[2] Graduate Student and Professors respectively, Department of Land, Air, and Water Resources University of California, Davis, CA 95616. e-mail: mmhynes@ucdavis.edu, rjzasoski@ucdavis.edu, csbledsoe@ucdavis.edu.

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

these belowground structures is difficult due to the interweaving of hyphae and soil particles, as well as small hyphae diameters (2-10 μm) (Allen 1991). Recent developments by Wallander and others (Wallander and others 2001) have made it easier to examine hyphae *in situ*. The use of sand-filled nylon mesh bags in soil near tree roots facilitates extraction and quantification of hyphal length and biomass.

Length is a common parameter used to quantifying fungal hyphae. Methods developed originally by Newman (1966) and modified by Tennant (1975) initially focused on quantifying root length. Over the last three decades, the equations developed by Newman and Tennant have been easily applied to quantify hyphal length and have been used frequently in conjunction with the gridline intersect method (GIM) (Bearden and Peterson 2000, Dighton and Skeffington 1987, Miller and others 1995, Nuemann and George 2005, Staddon and others 2003, Tisdall and Oades 1979). However, most studies combined GIM with hyphal staining using dyes (i.e., Trypan blue); this allowed for detection of lighter-colored hyphae. The procedure required extended microscope use.

Hyphae can be extracted from soil using the well-established filter method (Hensen and others 1974), followed by staining and either automated or manual quantification methods (Morgan and others 1991). More recently, as a way to quantify fungal growth, pharmaceutical and food industry researchers have analyzed hyphae growing in culture or contaminating food samples using automated and semi-automated programs in which some user input is required (Cox and others 1998, Packer and Thomas 1990, Tucker and others 1992). However, these automated and semi-automated programs are often expensive ($2,000-$13,000 USD) and sold as packages (i.e., microscope, computer, and software). Hyphae can be measured *in situ* (Lucas and others 2005) using minirhizotron tubes, a mini-camera, and WinRHIZO Tron software. However, one’s view of the hyphae present in the soil is limited to the small size of the camera window.

The capability to quantify hyphal length with more efficacy increases the value of studies evaluating the role of hyphae in nutrient and water uptake and subsequent transport to their mycorrhizal hosts. More importantly, a better understanding of hyphae effects (i.e., increased water uptake for hosts during drought) might help us understand the ability of oaks to survive in the Sierra Nevada foothills of Northern California.

In this method development and comparison, we used hyphal samples from a field study of multiple tree species. We compared the results of two methods for measuring hyphal length: (1) a semi-automated method using WinRHIZO Pro 2002©, and (2) an established manual method that relies on Newman and Tennant’s equations to quantify hyphal length. We examined accuracy and rate of data acquisition for each method.

Materials and Methods

Study Site

The field study was located at the Sierra Foothills Research and Extension Center (SFREC), Browns Valley, California, approximately 100 km northeast of Sacramento, California, U.S.A. The area is characterized by a Mediterranean climate, with cool, wet winters and hot, dry summers. The mean annual air temperature is

15°C, and the average precipitation is 73 cm (Dahlgren and Singer 1994). Soils at the SFREC are fine-loamy, mixed, thermic, Mollic Haploxeralfs and fine, mixed, thermic, Typic Rhodoxeralfs (Dahlgren and Singer 1994). The arborescent vegetation consists of blue oaks (*Quercus douglasii*), interior live oaks (*Quercus wislizeni*), foothill pines (*Pinus sabiniana*) and ponderosa pines (*Pinus ponderosa*). Grasses and forbs in this area include of *Bromus* spp., *Lolium* spp., *Madia* spp., and *Trifolium* spp. (Jackson and others 1990). We selected blue oak, interior live oak, and foothill pine trees in an area that has been ungrazed for ≥40 years. The ponderosa pines in this study were located in a nearby (~1.2 km) grazed area on a north-facing slope.

Experimental Design

The experimental design included four replicate mature trees of each of the four tree species. Hyphal in-growth bags were placed around each of the 16 tree species. Bags (5 cm circumference and 10 cm long) were constructed using 25µm nylon mesh; this created a root-restrictive structure that only allowed for penetration by hyphae. Each bag was filled with 300 grams of medium-course sand. The sand was leached, autoclaved and then amended with enough 0-10-10 (N-P-K) fertilizer to result in a phosphorus concentration of 100 mg P/kg sand. In order to discourage saprotrophic fungal growth, no carbon source was added to the bag. Four in-growth bags were vertically inserted 10cm into the ground at the canopy edge around each of the trees. Gravelly and cobbely areas were avoided. Bags remained in the ground for one year (April 2004 to April 2005).

In-growth bags were harvested, immediately freeze dried, and finally stored at -20 °C. For hyphal biomass, we thawed the bags, emptied each bag into a 500 mL wide-mouth container and shook the contents by hand for 15 seconds. This brief shaking allowed the hyphae to clump together for easier extraction. The sample was then sieved with a window screen (2 mm by 2 mm). The remaining hyphae on the screen were removed and the contents were sieved again to obtain more hyphae from the sample. The hyphae were then separated by hand from most of the organic matter, then weighed and stored once again at -20 °C.

A subsample of the hyphal sample was placed in methanol (MeOH) for ergosterol analysis. Placing the sample in MeOH allowed for some of the remaining sand particles or organic matter to become dislodged. A small subsample was removed from the ergosterol subsample. Several drops of deionized water were added to the hyphae, and the clumps were separated into 1-3 mm lengths using a scalpel. The water-hyphae mixture was filtered using a 0.22 µm nitrocellulose Millipore filter (Miller and Jastrow 2006). Hyphae on filters were then dried (60°C, 24 h) and transferred to a Petri plate (5.8 cm diameter). A transparent grid (~66 rectangles each measuring 4 mm x 6 mm) was then placed on top of the filter in the Petri plate.

Hyphal Length Analysis

Based on the method by Miller and Jastrow (2006), we developed a semi-automated analysis of hyphal length. Using a Nikon Stereoscopic Zoom Microscope SMZ1000 (Nikon Instruments, Inc., Melville, NY, USA) and a SPOT™ RT Camera, 20x magnification images were taken using SPOT™ RT Software v 3.4 (Diagnostic Instruments, Sterling, Heights, MI, USA). For each of the randomly selected hyphal in-growth bags evaluated, each rectangle of the of grid was photographed as a 1,600 x 1,200 pixels 'jpeg' image and labeled sequentially. Images were collected in black and white for greater contrast (*fig. 1a*) and analyzed using WinRHIZO PRO 2002© software (Arsenault and others 2002). An initial semi-automated analysis was performed and then refined by reanalyzing sections of the rectangle (*fig. 1b*).

The analysis performed by the WinRHIZO program follows a modified version of a non-statistical method presented at the American Society of Horticulture meeting (Arsenault and others 1995) and is briefly discussed in the WinRHIZO 2002a Basic, Regular, and Pro manual (2001). The length analysis relies on skeleton images or skeletonization to calculate hyphal length. Skeletonization uses an algorithm. Digital images are collected and simplified to a one-pixel line, which is recognizable for the algorithm and classification system (i.e., root length) (Himmelbauer and others 2004, Klette 2002) .

To minimize variation, the same images of the gridded Petri plate were then analyzed for hyphal length using GIM. Taking horizontal and vertical counts of hyphae that crossed the edges of each rectangle, the total number of hyphal crosses or intersections can be used to calculate hyphal length. The number of hyphal intersections occurring at the top and right side of each rectangle were totaled, which ultimately accounted for all sides of the grids. Total counts were used in two different equations. The GIM equations by Newman (1966) and its later-modified version by Tennant (1975) were developed for determining root length, but could be used to determine hyphal length and biomass (Miller and others 1995). Newman and Tennant's equations are as follows:

$$\text{Newman (1966): root length} = \frac{\pi \text{NA}}{2\text{H}}$$

$$\text{Tennant (1975): root length} = \left(\frac{11}{14}\right) * \text{grid unit*N}$$

Where 'N' in the count of the number of intersections across vertical and horizontal lines, 'A' is the area of the rectangle or grid, 'H' is the total length of the grid lines (length of grid rectangle multiplied by the number of grids), and 'grid unit' is the length of the gridded section. The counts and appropriate values for variables were inserted into each of the equations; hyphal length was determined for each sample. Data on hyphal lengths from each method and equation were analyzed statistically using a paired t-test in Systat 11 (Systat Software, Inc. 2004).

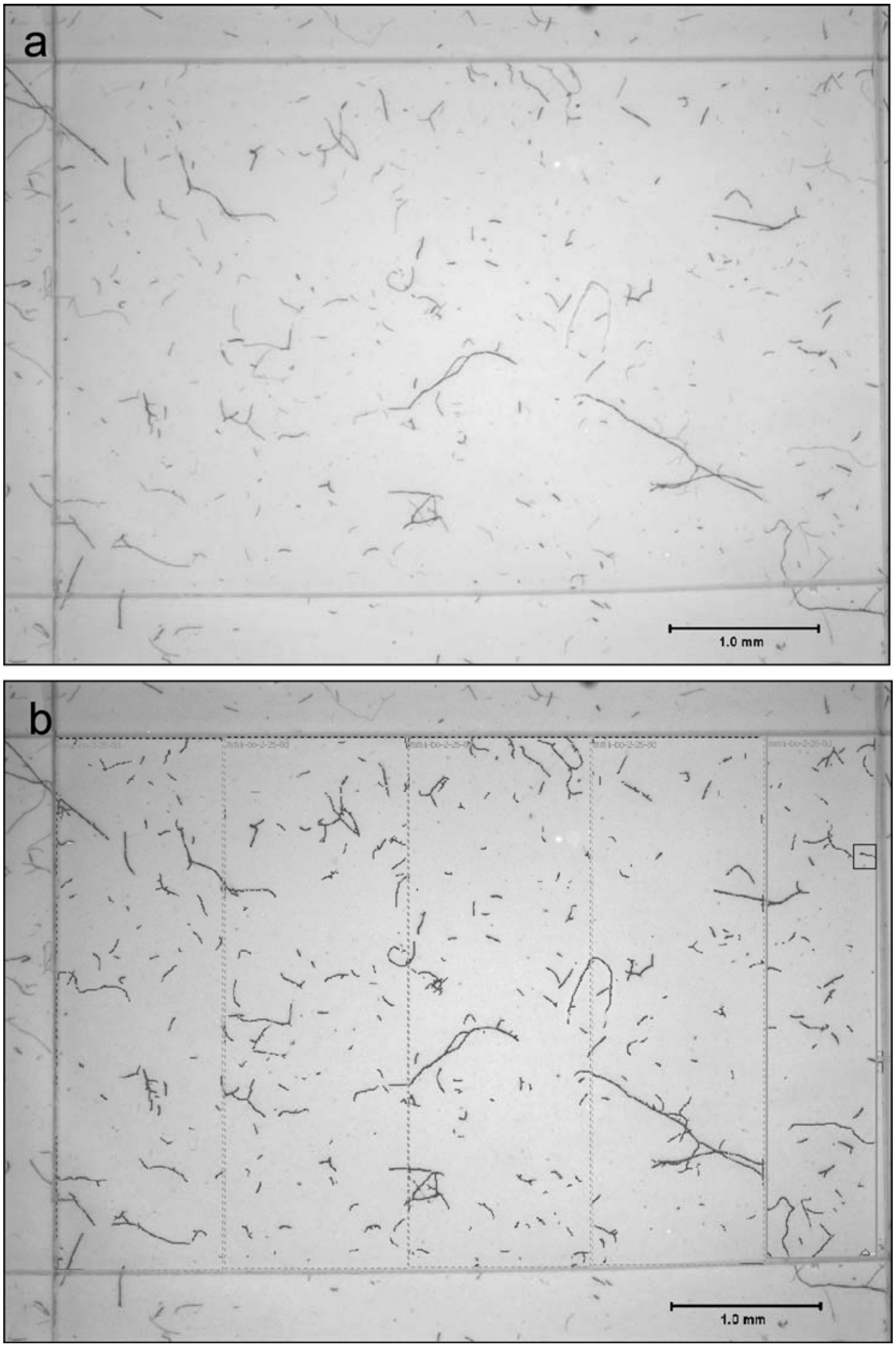

Figure 1—Images of a rectangular grid over a Millipore filter with hyphae before (a) and after (b) WinRHIZO Pro 2002© length analysis. Only the area inside the rectangular grid was analyzed for each picture. Hyphae in the sample shown are from a nylon mesh bag buried beneath a mature interior live oak tree.

Results

The image-capture process took approximately 1.5 to 2 hours per sample to achieve the correct image quality sufficient for analysis with WinRHIZO. Each image (rectangle on grid) took approximately 3 to 18 minutes to analyze, depending on two factors: (1) sub-sample size (i.e., more hyphae per rectangle equals longer analysis time), and (2) sample quality (how well the sample was subdivided into smaller pieces). On average, we collected 66 images per sample; this required an average of 8 minutes of analysis time of each rectangle. Overall, almost 9 hours per sample was necessary. In contrast, the use of GIM required only 15 minutes to analyze the entire Millipore filter (all 66 images) and ~3 minutes to enter the recorded counts into a spreadsheet using Newman and Tennant's equations. Analysis time using WinRHIZO was 30 times longer compared to using GIM and equations.

Results of hyphal length for the two methods and two equations are presented in table 1. To demonstrate accuracy of the method, data are presented as raw numbers and are not extrapolated for subsample weight, which would show differences between tree species. For the comparison, five random samples from five different trees were used to evaluate the methods. Using the GIM and Newman's equation resulted in the highest average measured hyphal length at 2.51 m (*table 1*). WinRHIZO and GIM with Tennant's equation resulted in similar average lengths of 2.27 m and 2.16 m, respectively.

Table 1—*Hyphal lengths (m) measured with WinRHIZO PRO 2002©, and grid-line intersect methods (GIM) length calculated using either Tennant's or Newman's Equation.*

	WinRHIZO Pro (m)	GIM -Tennant (m)	GIM - Newman (m)
Blue Oak 1	3.34	2.93	3.67
Blue Oak 2	2.87	2.88	3.55
Live Oak	2.40	2.26	2.40
Ponderosa Pine	1.29	1.19	1.32
Foothill Pine	1.44	1.54	1.61
Method Means ± S.E.	2.27 ± 0.397	2.16 ± 0.349	2.51± 0.482

The three different approaches were not significantly different (t*able 2*). Moreover, a high correlation ($r > 0.97$) exists between each method pair.

Table 2—*Methods were evaluated as pairs and sample means were compared using a Paired t-test with $p<0.05$ being significantly different ($n=5$). Correlation is also shown.*

	WinRHIZO Pro and Tennant	WinRHIZO Pro and Newman	Tennant and Newman
Paired t-test	p = 0.287a	p = 0.125a	p = 0.076a
Correlation	0.981	0.978	0.989

Discussion

The use of a semi-automated method, which involved use of a microscope, digital camera, and the program WinRHIZO to collect and analyze images, was not a more rapid and efficient alternative to the well-established GIM for determination of hyphal length. Our data supports the efficiency of the long-standing GIM and its associated equations by Newman (1966) and Tennant (1975). After three decades of use, the GIM and equations are still the most straightforward and efficient method to measure hyphal length. We recommend Tennant's equation rather than Newman's equation. We found that Newman's equation overestimated hyphal length compared to Tennant's equation. Since the correlation between WinRHIZO and Tennant's equation is slightly higher than the correlation between WinRHIZO and Newman's equation, we recommend an underestimation of hyphal length using Tennant's equation rather than overestimation of hyphal length using Newman's equation. Furthermore, the calculation and determination of numerical values for Tennant's equation is more straightforward than with Newman's equation.

In addition to analysis of the various methods, we discovered improvements to the GIM. We shortened microscope time required for GIM counts; our modification required only a few seconds of camera and microscope setup time compared to constant viewing of the sample through a microscope when GIM is used without the assistance of capturing images. A decrease in microscope time benefits researchers who are negatively affected by prolonged microscope use (i.e., nausea, eyestrain, or neck ache).

Species of fungal hyphae could not be determined using this method or any enumeration method. In oak woodlands, oaks and pines form ectomycorrhizal fungi (ECM) while grasses and forbs form arbuscular mycorrhizal fungi (AMF) associations. We were able to determine if the hyphal samples were saprotrophic and ECM versus AMF by observing the presence or absence of septa (cross-walls in the hyphae). Septa are not found in AMF hyphae. ECM (septate hyphae) were generally larger in diameter (4-6µm) than AM hyphae.

The use of an expensive automated program may be a preferable investment for laboratories that frequently quantify hyphal length. However, our results suggest that laboratories with smaller samples sizes, should use the GIM. Furthermore, a microscope, computer, and camera are probably more available and accessible than expensive imaging equipment and software.

Summary

Our comparison of methods to quantify hyphal length showed that using the grid line intersect method in conjunction with Tennant's root length equation was the optimum approach. In the future, WinRHIZO and other semi-automated or automated programs may improve and become faster and more efficient processes for measuring hyphal length. As new approaches begin to improve the efficiency of hyphal extraction from media, researches will require complementary automated programs to measure hyphal biomass. Until then, due to its efficiency and accuracy, the use of well-established fungal length quantification methods with the addition of minor enhancements (e.g., use of dissecting microscope images) is recommended for research on tree species and their associated hyphae. The ease of extracting and quantifying fungal hyphae from soil determines the speed at which we obtain knowledge concerning below-ground fungal processes such as seedling and sapling mycorrhizal inoculation, as well as nutrient and water transport via hyphae to hosts. Relating these findings at an ecosystem level can be an arduous task, but improving quantitative methods may allow for more insight into oak woodland regeneration and management.

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Continue

Planning, Conservation, and Policy

Continue

The Impact of West Nile Virus on Birds in California's Hardwood Rangelands[1]

Thomas Scott,[2] Pey-Yi Lee,[3] Kerry Paggett,[4] Ryan Carney,[3] Stan Husted,[3] and Walter Koenig[5]

Abstract

West Nile virus has undergone an unprecedented rate of infection in North America, sweeping from New York to California in four years. It attacked an exceptionally broad range of hosts/vectors over a broad geographic area. In 2004, the California Department of Health Services received approximately 98,000 reports of dead birds, representing tens of millions of birds killed by West Nile virus in California. The rates of dead bird reports in California Hardwood Rangelands varied from 54 ± 11 birds/km2 in the upper Sacramento River Valley to 3.7 ± 0.8 birds/km2 in the southern coastal foothills. Overall, about 80 percent of hardwood rangelands were in areas of moderate to high rates of West Nile outbreak. Areas suffering the highest rates of mortality had primarily blue oak and valley oak woodlands, and bird species in blue oak woodlands suffered the greatest potential exposure to West Nile virus.

Keywords: Bird deaths, hardwood rangelands, West Nile virus.

Introduction

California's hardwood rangelands have been challenged by three decades of suburban growth (Bolsinger 1988, Scott 1993, Wadell and Barrett 2005), focusing state woodland policies on habitat conversion and loss (State of California Resources Agency 2003, Hilty and others 2006). Wildlife diseases, in contrast, have failed to generate the global concern directed at suburban sprawl, because they typically occur as localized problems. That changed in 2004, when West Nile virus created the greatest mortality event in the recorded history of California wildlife. The 2004 outbreak defined a new role for infectious diseases in hardwood rangeland ecology and management. In this paper, we summarize the impact and pattern of this emerging disease on the state's woodland bird species.

West Nile virus (WNV) swept North America in four years, infecting the largest number of wildlife species over the greatest geographic area ever recorded for any epizootic. Mortality has been documented for more than 260 native and 110 exotic/domestic species in North America, ranging across all terrestrial vertebrate groups (Komar and others 2003, Marra and others 2004, USGS 2005). Given the wide range of taxa affected by the virus, it appears reasonable to assume that some level of morbidity and mortality occurred in every vertebrate species exposed to the virus and that the signal of this impact should be evident in the wake of the epizootic. Nevertheless, the impact of WNV has been difficult to document in wildlife populations (Caffrey and Peterson 2004).

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[2] Integrated Hardwood Range Management Program, Dept of Environmental Science, Policy, and Management, University of California, Berkeley; and Center for Conservation Biology, University of California, Riverside, CA, 92527.

[3] Department of Earth Sciences, University Of California, Riverside, CA, 92521.

[4] California Department of Health Services, Richmond, CA, 94720.

[5] Museum of Vertebrate Zoology, University of California Berkeley, CA, 94720.

West Nile virus is spread primarily by mosquitoes, which become infected with the disease after a blood meal on an infected host. The mosquitoes can then pass the virus onto other vertebrates in subsequent blood meals, and in low percentages onto their own offspring. The amount of virus present in a host's blood (viremia) is critical in its transmission to mosquitoes, as is the ability of the virus to move from the gut to the salivary glands of the mosquito before the mosquito takes a second blood meal. West Nile virus is an old world flavivirus, similar to the encephalitis viruses already found in California and the United States. However, a new strain of WNV, which appeared in localized outbreaks in Israel and Europe in the late 1990s, causes higher levels of viremia in some species of birds (Brault and others 2003, Reisen and others 2005). Hence when WNV reached North America, it could be more efficiently spread among vertebrates with no previous exposure or resistance. WNV can also be passed from prey to predator and between individuals in close contact when the virus is ingested (McLean and others 2001, Nemeth and others 2006). Hence WNV has a number of pathways for movement, amplification, and persistence.

A number of North American birds showed little or no resistance to WNV when it was discovered in New York in 1999 (Komar and others 2003). American crows (for scientific names see table 1) and other peri-urban bird species helped to spread the disease in urban and suburban areas (Reisen and others 2005). It was detected for the first time in California in July 2003; by October 2003 it was detected in the cis-montane region of Southern California. A year later, it had been reported from all of the counties in California.

After its discovery, West Nile virus was systematically monitored across the United States, and an extensive surveillance program was instituted by the California Department of Health Services (CDHS 2003). The CDHS West Nile Virus Task Force collected more than 98,000 dead bird reports in 2004, providing data on the spread and impact of the disease on birds in California. These data allow us to examine the impact of West Nile virus on the woodland bird species of California. Here we attempt to estimate the overall impact of WNV on woodland bird species and to describe the pattern of the 2004 WNV outbreak across California's hardwood rangeland.

Methods

We used dead bird data from the California Department of Health Services West Nile Virus Hotline (hereafter referred to as the Hotline) to calculate the impact of West Nile Virus on woodland birds in California. The Hotline, a telephone and Internet system, received reports of dead birds from individuals across the state of California. The primary goal of the Hotline was to guide the WNV dead bird testing program, providing early detection of WNV as it moved into communities across the state. A secondary goal of the system was to use dead bird reports (primarily crows and other corvids) to monitor the patterns of WNV outbreaks (CDHS 2003). Citizens were urged to use the system with public service announcements, but many reports came through local animal damage control agencies and mosquito abatement districts. Information flowed through a central CDHS office in Richmond, California. Callers provided the street addresses, dates, numbers, and in a surprising number of cases, the species of dead birds they found around their neighborhoods and houses. From January to October 2004, approximately 77,000 callers had reported approximately 90,500 bird deaths. At the height of the 2004 WNV outbreak, CHDS employed more than 20 staff members to receive phone calls, assisted by 8 volunteers from the UC Cooperative Extension Master Gardener's Program in Riverside County.

The CDHS dead bird reports were voluntary and provided a large but non-systematic sample of the actual mortality caused by WNV. Several authors (Balcomb 1986, Philibert 1993, Tobin 1990, Ward 2006) have identified biases in dead bird detection, including (1) bird species are differentially detectable, given their size, plumage, habitat use/occurrence; (2) bird carcasses can be detected for different periods of time, based on decomposition conditions (e.g., insects, moisture), and vertebrate scavengers; (3) birds can die in places where they will not be detected; (4) the number of observers impacts the detection rates and estimates of density. Sick birds also can be removed from detection when they are eaten by predators or when they move away from their point of infection. Ward and others (2006) also points out that not all detections are reported. In our case, each dead bird report required (1) that the caller knew about the Hotline or was directed to the Hotline by a third party; (2) that callers were motivated to provide information; and (3) that callers succeeded in getting their information into the system. This was an exceptionally large task with a large number of potential disruptions. Nevertheless, the Hotline received more than 90,000 calls during the 2004 WNV outbreak, and this volume of dead bird data allowed us to partition and sub-sample the data to detect patterns of the epizootoic.

We geo-coded the addresses provided by callers using ARCGIS© software in order to describe the spatial pattern of bird mortality in California woodlands. We grouped these data points into sample units by census tracts. Because raw data was biased by the number of observers available at any location, we standardized observations across sample points by dividing the number of dead bird reports within each census tract by the number of single-family detached-housing units within its boundaries. We used single-family detached houses rather than total households because very few records came from multiple family housing. Data on single-family housing were taken from Tiger files of the U.S. Census Bureau 2000 census (U.S. Census Bureau 2000). In order to make these numbers ecologically relevant, we created a reference unit of dead bird reports per 1,000 houses, which is equivalent to an area of approximately 250 acres or 100 hectares, based on average housing densities in California. All dead bird numbers in this paper are reported in these units. Next we divided the observed rate of reporting by 0.27 for urban areas and 0.1 for rural areas to account for detection and reporting errors (Ward and others 2006).

We then corrected these estimates using the ratios of West-Nile positive dead birds to the total number of dead birds tested between 1 January and 27 October 2004 by the CDHS WNV Surveillance program. During this period, CDHS tested approximately 5,034 dead birds for WNV. Of these birds, 62 percent (3,105) tested positive for WNV (Riesen 2005).

There remain several shortcomings of this protocol. The system was designed to detect the initial cases of the disease and thus some birds were tested from areas before the disease outbreak occurred as well as after WNV outbreaks had subsided in October. Furthermore, testing ceased in areas with particularly high rates of bird death because the number of dead birds available for sampling threatened to swamp the testing system. Hence, the reported proportion of WNV-positive birds among dead birds submitted for testing is a conservative estimate of the rate of mortality. In addition, there is no test for the absence of WNV. Birds that tested positive for WNV were unambiguous and provided surveillance information for CHDS program; however, birds that were scored negative included both uninfected birds and birds that had been killed by WNV where the virus escaped detection. Finally, some portion of the birds with the virus present may nonetheless have died of other causes unrelated to WNV, creating an over-estimate of the mortality caused by WNV.

We used USGS Breeding Bird Censuses (BBC; http://www.pwrc.usgs.gov/birds/bbc.html) to estimate the relationship between bird density and the corrected dead bird reporting rates in sample areas. These censuses were conducted on 10-ha plots (n=247) across California, starting in 1937. They provide the broadest estimates of the density of breeding pairs of California species in urban and woodland areas. In addition, there are several estimates of urban bird densities in the published literature with numbers ranging from 1,000 (ref) to 1,300 (ref) breeding pairs/100 ha. We first calculated worst-case, median-case, and best-case estimates of the impact of West Nile virus in urban areas for all species combined. We then calculated the same three values for species in which reasonable data exists to estimate their urban densities (number of breeding pairs and offspring per year per unit area) and their mortality to WNV.

Results and Discussion

Dead Bird Reports

Californians reported approximately 98,500 dead birds to the CDHS West Nile Virus Hotline from January through October 2004. About 80 percent of these reports came from single calls to the Hotline, while 20 percent came from multiple reports from single callers. Approximately 24 percent of these reports came from hardwood rangelands, 60 percent from suburban communities in Southern California, 10 percent from suburban communities in Northern California, and the rest from mountain and desert areas.

Correcting for Detection and Reporting Errors

If the numbers of dead bird reports is corrected to account for detection and reporting errors, then the corrected estimate of WNV-related deaths in California rises to about 640,000 birds killed in the areas where reporting occurred. The corrected factors (0.27 for urban and 0.1 for rural) should be considered conservative because both the detection and reporting rates in California dead bird reports are likely to be lower than those of Ward and others (2006), since their rates were calculated for dead crows with contact information printed on the carcasses placed in observable locations by researchers rather than dying in natural situations. Most passerines are much less conspicuous than crows and are likely to die in inconspicuous refuges. In addition, most dead bird records came from callers who were motivated by concern over WNV more than the death of yard-birds (T. Scott, unpublished data). Indeed, 94 percent of individuals filing dead bird reports made no subsequent reports to the Hotline, whereas, about 1 percent of callers made >3 calls to the Hotline. Furthermore, a substantial proportion of individuals failed to contact the Hotline, either because they did not know the Hotline existed, failed to connect to the Hotline, or were unmotivated to call. Finally, public information was focused on a subset of birds (corvids, raptors, icterids, finches, and sparrows), reducing the extent and numbers of other taxa reported. The number of callers who reached the WHV Hotline but did not leave any information (approximately 35 percent) provides a minimum estimate of the number of individuals who observed bird deaths but failed to provide information. At the present time, other factors cannot be estimated.

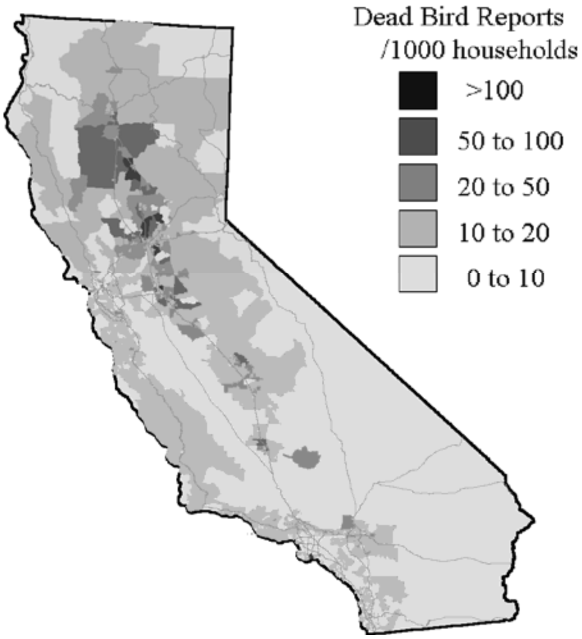

Figure 1—Statewide pattern of the 2004 California Department of Health Services West Nile Virus Hotline dead bird reports (non-crow), grouped by U.S. Census Bureau 2000 census tracts (see text). Densities are reported as dead birds per 1,000 households, approximately equivalent to dead birds per 100 ha. Interstate and major state highways are shown in gray.

Comparing Dead Birds Records With Birds Tested for WNV

Sixty-two percent of dead birds tested in California in 2004 were positive for WNV (Reisen 2005). However, birds from areas and dates inclusive of WNV outbreaks (15 May to 30 September) had an overall higher rate (68 percent) of WNV-positive birds (2,198 positive results among 3,233 birds). The proportion of WNV-positive dead birds ranged from 35 percent for dead raptor (hawks and owls) species to 100 percent of western bluebirds (*table 1*). About 60 percent of all non-corvid passerine birds tested positive for WNV; however, only about 50 percent of common backyard species including house sparrows, house finches, and California towhees) were positive for the virus, compared to 68 percent of less common species.

We assume that the proportion of positive/tested birds was a function of (1) the prevalence of WNV, (2) the exposure and infection rate of each species, (3) the susceptibility of each species to WNV-related mortality, and (4) the likelihood that birds submitted for testing died of other causes. Dead raptors, because of their size, color, and prestige, may have drawn more attention; hence raptors may have been submitted more frequently than passerine birds, and raptors that died of non-WNV related causes may have been better represented than passerine species that died of non-WNV related causes. Even with this bias, species of dead raptors had higher proportions of WNV-positive individuals than would be predicted, based on studies of experimental infection (Nemeth and others 2006a, 2006b).

Table 1—*Proportion of individuals that tested positive for WNV, adjusted for dates when West Nile virus was present in sampling areas. Calculated from the subset of bird tested within the WNV outbreaks (15 May to 30 September).*

Species	Proportion WNV-Positive [a]	Dead Birds Tested
Western Bluebird (*Sialia mexicana*)	1.00	6
Brewers Blackbird (*Euphagus cyanocephalus*)	0.91	12
Yellow-billed Magpie (*Pica nuttalli*)	0.87	288
Black-billed Magpie (*Pica pica*)	0.85	7
Black-headed Grosbeak (*Pheucticus melanocephalus*)	0.81	11
American Kestrel (*Falco sparverius*)	0.8	15
Western Scrub-Jay (*Aphelocoma californica*)	0.79	630
Mourning Dove (*Zenaida macroura*)	0.72	11
American Robin (*Turdus migratorius*)	0.70	24
Steller's Jay (*Cyanocitta stelleri*)	0.69	85
American Crow (*Corvus brachyrhynchos*)	0.69	1711
Red-tailed Hawk (*Buteo jamaicensis*)	0.66	32
Acorn Woodpecker (*Melanerpes formicivorus*)	0.60	10
House Sparrow (*Passer domesticus*)	0.54	37
California towhee (*Pipilo crissalis*)	0.53	15
Black Phoebe (*Sayornis nigricans*)	0.50	6
Northern Mockingbird (*Mimus polyglottos*)	0.50	8
Western Screech Owl (*Megascops kennicottii*)	0.50	8
House Finch (*Carpodactus mexicanus*)	0.46	61
Cooper's Hawk (*Accipter cooperii*)	0.40	51
Common Barn Owl (*Tyto alba*)	0.38	47
Red-shouldered Hawk (*Buteo lineatus*)	0.30	23
Great Horned Owl (*Bubo americanus*)	0.29	17
Common Raven (*Corvus corax*)	0.25	108

Experimental infections of birds indicates that magpies and other corvids have lower resistance to WNV than many species of passerine birds (Komar and others 2003); this susceptibility is mirrored in the CDHS data by high values for all species of corvides with the exception of common ravens, which did not exhibit high prevalence of WNV. The number of WNV-positive house sparrows was far higher than would be expected, given their moderately low rates of mortality during experimental infections with WNV (Reisen 2005). House finches had a lower rate of WNV-positive birds than house sparrows, even though they appear to be more susceptible to the WNV (Reisen 2005). These results suggest that common species may have had higher proportions of non-WNV related deaths reported to the Hotline because they occur in much higher densities around suburban housing.

If we assume that the proportion of WNV-positive individuals represents a reasonably close estimate of the proportion of WNV-related deaths in the dead bird reports, then it is necessary to reduce the number of reports by the values reported in table 1. For species with small sample sizes, we assume that the overall proportion of WNV-related deaths was 68 percent of the sample for non-corvid passerines and 35 to 40 percent for non-passerines. If the ratio of WNV-positive dead birds to total dead birds is applied by species to the dead bird reports, then the total number of dead bird reports to overall estimates of dead birds reports involving WNV would drop to 61,500. With this as a corrected estimate of dead bird calls, the corrected estimate of

WNV-related deaths in California drops to about 400,000 birds killed in areas where reporting occurred.

Sampling Units for Dead Bird Reports

Almost all dead bird reports (>99 percent) were from single-family detached housing properties, such that sampling efficiency is linked to housing density. Approximately 51percent of 2000 census tracts in California had suburban housing densities (5 to 18 dwelling-units/ha); however, these census tracts cover only about 3.3 percent of the state's land areas. An additional 0.3 percent of the land area has urban housing densities (>18 units/ha) and 5 percent is in ranchettes (1 to 5 units/ha). The majority of the state land area (91.4 percent) is in census tracts with rural/wildland densities of <1 unit/ha. If all suburban housing areas are considered as the sample area, then dead bird reports covered approximately 13,400 km^2 or about 3.5 percent of the land area of California.

In order to report dead birds from rural clusters of housing, it was necessary to report data by housing unit rather than aerial measurements. In suburban census tracts (n=3551), density of housing was 10.01 + 3.3 units/ha, or 1,000 houses to 100 ha. The reporting rates were also equivalent with 5.2 + 8.0 reports/1,000 households and 5.1 + 8.4 reports/100 ha (R2 = 0.83; p < 0.001). Because these two units were equivalent, we used dead bird reports/1,000 houses to analyze rural/wildland census tracts where report/ha becomes less useful because of the sparse and highly variable numbers of observers.

Birds Reported Per Sample Unit

Statewide, the number of birds/1,000 houses (100ha) averaged 7.1 + 37.2 (SD) among U.S. Census tracts (n= 7,037). Corrected for reporting rates and non-WNV dead, a minimum estimate would be a statewide average of 0.18 dead birds/ha in urban (sampling) areas. This sample distribution, however, is a negative binomial, and the median of 5.01 dead birds/1,000 houses is a better descriptor for WNV dead bird reporting rates. About 17.6 percent of census tracts had >10 dead bird reports/1,000 houses and 0.8 percent of census tracts had >50 dead bird reports/1,000 houses. The highest reporting rates were grouped around 300 dead bird/1,000 houses, or 3 dead birds/ha, while 0.25 percent (35) of census tracts had reporting rates >100 dead birds/1,000 houses. About one-third of the dead bird reports could not be geo-referenced, so it is possible that the number of census tracts without dead bird reports could be substantially lower than 18 percent, and the median number of dead birds/1,000 households could have been up to a third higher (~7 reports/1,000 houses).

Non-Crow Deaths Per Sample Area

The number of non-crow bird deaths/1,000 houses was substantially lower than total (with crows), averaging 3.2 + 6.7 (SD) among census tracts (n=7,037). Corrected for reporting rates and non-WNV-positive dead, yields a minimum statewide estimate of 0.08 non-crow deaths/ha in urban (sampling) areas. The median of non-crow dead reported was 1.7 birds/1,000 houses. About 17.6 percent of census tracts had reporting rates >10 dead birds/1,000 houses, and 0.3 percent of census tracts had reporting rates >50 birds/1,000 houses. The highest reporting rate was around 60 dead birds/1,000 houses.

Non-Crow Mortality in Suburban Communities

There are relatively few estimates of urban bird densities, but Breeding Bird Census (BBC) data suggests that the minimum number of breeding pairs of California birds in suburban areas is probably on the order of 660 pairs/100 ha plot (based on an average of 81 + 14 (SD) pairs/10 ha plots in five BBC plots). The maximum density of breeding pairs is more variable. However, the maximum density of suburban birds is unlikely to exceed 1,400 pairs/100ha found in riparian oak woodlands (based on 140 + 63 singing males/10 ha plot; n=14). The density of suburban birds reported in the literature is intermediate at about 1,100 pairs/100ha (Blair 1994).

Given these densities, the overall density of birds in reporting areas could have ranged from 1,950 birds/100 ha (600 equal sex ratio, 1 young/pair) to 5,600 (1,400 pairs, equal sex ratio, averaging two offspring per pair), with an intermediate density of about 3,800 birds/100 ha (1,100 pair/ha, 1.5 young per pair). The census tract average for non-crow dead bird reports can be adjusted up to about 8 dead birds/100 ha, given minimum error in detection and reporting. If these numbers are correct, then minimum proportion of non-crow birds (all species combined) killed across census tracts in urban areas could have ranged from about 0.03 percent to about 0.1 percent across the state. Census tracts in the areas with the highest reporting rates could have suffered a minimum of 2 percent death rates. Census tracts with exceptionally high reporting (top 0.2 percent) could have suffered minimum mortality rates of 2 to 25 percent.

Geographic Variation in Reporting Rates

Suburban areas in the Great Valley had the highest reporting rates for non-crow bird deaths during 2004 (*table 2*), with an average of 21.8 + 17.9 reports/ha. At the other extreme, the coastal areas of Southern California had reporting rates of 0.9 + 1.3. In general, low-elevation interiors area of California with large amounts of surface water had the highest reporting rates to the WNV Hotline; areas that were either dry (deserts) or cool (Sierra Nevada and coastline) had far lower rates.

Table 2—*Regional distribution of dead birds reported to the West Nile Virus Hotline by U.S. Census Tract in California (January to October 2004). Averages represent observed dead-bird-reports/1,000 households.*

Region	Urban Rates Mean ± SD (n)	Rural Rates Mean ± SD (n)
Central Valley		
Northern	21.8 + 17.9 (12)	19.7 + 15.5 (62)
Central	6.0 + 6.0 (251)	10.2 +17.4 (545)
Southern	5.5 + 3.4 (74)	8.8 + 7.9 (250)
Coast Ranges		
North	3.9 + 4.1 (26)	6.3 +4.0 (106)
Central	2.4 + 2.4 (59)	4.3 +3.0 (155)
Sierra Foothills		
Northern	3.5 +1.8 (5)	5.6 + 2.8 (75)
Southern	4.6 + 1.8 (7)	3.1 + 2.4 (14)
Southern California		
Interior	12.5 + 14.7 (390)	19.7 + 68.8 (522)
Coastal	0.9 + 1.3 (396)	11.3 + 18.6 (459)
Northeastern California	5.0 + 2.4 (9)	4.3 + 3.5 (16)
San Francisco Bay Area	1.4 + 1.9 (612)	3.8 + 7.8 (215)

Overlap Between Hardwood Rangelands and WNV

About 84 percent of California's hardwood rangelands was within 10 km of a reported WNV-positive dead bird. More important, 27 percent of hardwood rangelands occurred within census tracts where the strongest outbreaks of WNV were recorded (*table 3*). Blue oak and blue oak/pine woodlands had the highest overlap with WNV outbreaks (40 and 34 percent), while coastal oak and valley oak woodlands had the lowest overlap (5 and 1 percent of their respective areas). Valley oak woodlands have not been mapped for Central Valley riparian areas such as the upper Sacramento River. These areas had the highest recorded levels of dead birds and were probably the most heavily affected by West Nile virus. All of the highest areas of outbreak occurred within hardwood rangelands in areas dominated by blue oak woodland.

Estimating the impacts of WNV on woodland birds

The dead bird data area may be insufficient to estimate the population consequences of WNV for most woodland species, with two exceptions: the western scrub-jay and yellow-billed magpie. Reported deaths of both species were concentrated in the northern and central parts of the Central Valley, with 5 to 10 times the level of mortality found in coastal regions.

For western scrub-jays, it appears populations may have suffered over 50 percent mortality in areas of the Central Valley (*table 3*), and probably suffered local extirpations in all regions in which they occur. Reported mortality was far lower in coastal area (<1 percent), and was relatively low (<10 percent) in the central coast ranges, northeastern California, Southern California interior, and the southern Sierra foothills. Statewide, we estimate that this species suffered a minimum 2 percent population decline from WNV.

Table 3—*Regional distribution and estimated mortality of western scrub-jays based on dead birds reported to the West Nile Virus Hotline (January to October 2004). The number of U.S. Census Tracts in each sample are listed in table 2. High, intermediate, and low population densities are taken from literature (Curry and others 2002) see text. Estimate mortality rate (Est.) is based on reporting rates (0.27), WNV-positive rates (0.80), proportion of records geo-referenced (0.7).*

Region	**Urban rate[a]**	**Rural rate[a]**	**Mean reported mortality[a]**	**Est. dead[a]**	**Percent dead by population density**		
					High	**Int.**	**Low**
Central Valley							
Northern	4.7 ± 3.1	6.6 ± 4.5	6.3	26.9	9.8	19.2	29.9
Central	1.0 ± 1.1	1.7 ± 3.8	1.5	6.4	2.3	4.5	7.1
Southern	1.1 ± 1.2	2.0 ± 2.8	1.8	7.5	2.7	5.4	8.3
Coast ranges							
Northern	0.3 ± 0.7	0.8 ± 1.2	0.7	2.9	1.1	201	3.2
Central	0.1 ± 0.3	0.3 ± 0.6	0.3	1.2	0.4	0.9	1.4
Southern	0.1 ± 0.2	0.1 ± 0.3	0.1	0.2	0.1	0.2	0.3
Sierra foothills							
Northern	0.3 ± 0.5	1.1 ± 1.3	1.0	4.4	1.6	3.1	4.9
Southern	0.1 ± 0.5	0.5 ± 0.6	0.6	2.7	1.0	1.9	3.0
NE California	0.5 ± 0.8	0.6 ± 0.9	0.6	2.4	0.9	1.7	2.6
S interior	0.2 ± 0.5	0.5 ± 1.0	0.4	1.7	0.6	1.2	1.8
SF Bay area	0.1 ± 0.2	0.2 ± 0.7	0.1	0.5	0.2	0.3	0.5

[a] number of dead birds per 1000 houses or 250 ha.

Overall mortality among yellow-billed magpies, a California endemic, is more difficult to quantify because they nest in aggregations and often flock during the non-breeding season. However, the highest reported rates of magpie deaths (163 dead birds/1,000 houses in the central portion of the Central Valley, 49 dead-birds/1,000 houses in the northern Central Valley) would be sufficient to cause extirpation in typical population densities of the species (Reynolds 1995). The median reported rate of magpie deaths in the Central Valley census tracts (2.1 dead birds/1,000 houses) would result in a 40 percent decline in a typical population (6 pairs/100 ha) of this species.

Conclusions

The overall distribution of dead bird reports suggests that West Nile virus spread across the state but did not have a uniform impact across the state's hardwood rangelands. Dead bird reports were most frequent in the Central Valley, but appear to have been concentrated in hotspots that occurred in all types of hardwood rangeland. Some of these hotspots were sufficiently severe to cause local extirpations in at least two species of corvids, the western scrub-jay and the endemic yellow-billed magpie. At least 13 other species (*table 1*) also exhibited sufficiently high numbers of dead birds that tested positive for the presence of WNV that they are also likely to have suffered local extirpations. However, the majority of areas in California had dead bird reporting rates that would suggest mortality rates of <10 percent, which is perhaps why large-scale population declines were not reported among birds California's hardwood rangelands in 2004. The greatest numbers of dead birds were reported from the areas with the hottest summertime temperatures. High ambient temperatures increase the efficiency of mosquito transmission of WNV and shorten the development time of mosquitoes (Reisen and others 2006), which provides a plausible explanation of why hardwood rangelands in the Central Valley suffered the greatest impact of WNV and may be more susceptible to future invasion of mosquito-born viruses such as dengue or malaria.

Table 4—*Regional distribution of dead yellow-billed magpies reported to the West Nile Virus Hotline by U.S. Census Tract in California (January to October 2004). Rates are dead magpies reported per 1000 households.*

Region	Urban Rate	Rural Rate	Max. Rate
Central Valley			
Northern	8.90 + 10.5	5.2 + 9.54	48
Central	0.70 + 1.45	2.3 + 11.01	163
Southern	0.06 + 0.42	0.16 + 1.20	15
Central coast ranges	0.05 + 0.25	0.06 + 0.25	2
Northeastern California	0.60 + 1.22	0.04 + 0.14	3
San Francisco Bay Area	0.05 + 1.10	0.03 + 0.20	29

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Continue

The Economic Drivers Behind Residential Conversion in the Oak Woodlands[1]

William Stewart,[2] James Spero,[3] and Shawn Saving[4]

Abstract

Acre for acre, oak woodlands provide habitats for a greater range of wildlife species than grasslands and irrigated agricultural lands. Oak woodlands also are highly valued as open space around residential development. The rich habitat diversity and the physical attractiveness drives residential interest in living in or adjacent to oak woodlands as well as preservation interest in maintaining oak woodlands without an overlay of residential land uses. Numerous state and local regulations are being implemented to balance these competing goals. California's growing metropolitan population will continue to drive both the demand for new housing sites as well as more permanent open space near metropolitan areas. This paper analyses the spatial patterns of residential conversions to identify the key economic drivers behind residential conversion in the oak woodlands at the regional level. Using spatially explicit Census and land cover data, we mapped current residential densities within oak woodlands and other vegetation types for 1990 and 2000. We combined these data with real estate sales data to map regional patterns of high- and low-cost residential areas, grazing land, and public open space. Land surrounding San Francisco Bay, while highly desirable to potential residents, will not absorb much additional residential development as most is protected as public or privately owned open space. It is more probable that the growth pressures will be realized in areas further away from the San Francisco Bay in areas currently characterized by low-density residential development or smaller ranches.

Keywords: Demographics, economics, oak woodlands, real estate, residential land use.

Introduction

If historical land use trends continue, development is expected to impact around 500,000 acres of hardwood woodlands over the next 40 years (FRAP 2003a). Each county in California has taken a different approach towards balancing the demand for new residential development and preserving the values that open space provides to existing residents (Giusti and Merenlender 2002; Saving and Greenwood 2002; Thompson, Noel, and Cross 2002). Given that the demand for new residential parcels in the hardwood woodlands comes from both existing residents who will trade longer commutes for a woodland-dominated neighborhood and people relocating to new areas, it is important to understand the larger regional patterns of development pressures and open space values across Northern California (Mayer and Somerville 2000; Merenlender et al. 2005). The extent and the pattern of conversion from current uses to more residential uses will affect wildlife populations, open space values to

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[2] Cooperative Extension Specialist, University of California Berkeley, 137 Mulford Hall, MC 3114, Berkeley, CA 94720-3114, 510-643-3130. e-mail: stewart@nature.berkeley.edu.

[3] Research Program Specialist, California Department of Forestry and Fire Protection, PO Box 944246, Sacramento, CA 94244-2460, 916-324-7185. e-mail: james.spero@fire.ca.gov.

[4] GIS Specialist, Kansas Geological Survey, 1930 Constant Ave., Lawrence, KS 66047. 785-864-2094. e-mail: saving@kgs.ku.edu.

local residents, and other environmental attributes. The challenge is to improve our understanding of the regional trends driving residential conversion pressures, as well as the opportunities to ensure socially desired outcomes.

Methods

Developing a standard regional framework requires the use of standardized data sets. Three different data sets are used in the analysis. The first is the FRAP's (Fire and Resource Assessment Program) statewide analysis of population densities across all land cover types (FRAP 2003a). The second is the household income data from the 2000 Census, as it provides a measure of the location of households with the high incomes necessary to buy homes on large lots in California. The final data set is the ZIP code based real estate data on home sizes and prices in the major metropolitan areas of Northern California.

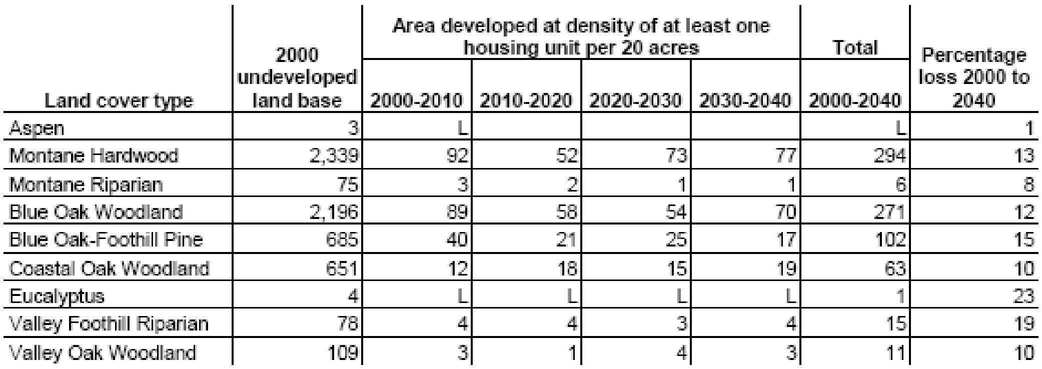
A simple and fairly accurate spatial projection of future urban and exurban residential land use can be developed by projecting historic trends out over the next few decades. Housing density within existing Census blocks can be determined by analyzing the "Year House Built" answers in the 2000 Census (U.S. Census Summary File 3, 2003). This approach was used by Duane in the Sierra Nevada Ecosystem Project (Duane 1996) and more recently applied statewide (FRAP 2003a). FRAP's "share of growth" model allocates countywide population projections to a finer spatial scale (i.e., census block group parts) by distributing California Department of Finance county population projections to census block group parts as a linear function of the share of growth in the preceding decade. Using current Census blocks as the consistent geographical unit allows for an accurate presentation of historical trends as well as a solid basis for making forward looking projections of land use changes.

The FRAP Assessment uses the census data model, referred to as the "Projection of Development," to estimate the extent of future development on all current vegetation types that were published in the FRAP Assessment. "Development" is defined as housing density of one or more houses per 20 acres. FRAP uses the one house per 20 acre threshold as it signifies the point where the existence of houses changes our fire suppression strategies and where there may be a significant level of watershed or habitat impact.

Above this threshold, 'rural residential' refers to areas with average lot sizes ranging from 5 to 20 acres, 'interface' refers to areas with average lot sizes ranging from 1 to 5 acres, and 'urban' refers to areas with average lot sizes of less than one acre. This methodology was first developed to explore development and fire trends on 1945-era Oak Woodlands of the Northwestern Sierra Nevada Foothills (Spero 2001). The primary purpose was 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. It is important to note that this fairly low density for 'developed' refers to far fewer houses per acre than the common view of developed, referring to subdivision densities in which average lot size is one acre or less. (e.g., Landis and Reilly 2003).

A map of these projections is available in the online version of the FRAP Assessment (FRAP 2003b). Table 1 summarizes the acres of potential conversion by different types of hardwood vegetation types. Blue oak woodlands constitute about half of the projected change.

Table 1—*Projected area* and percentage of current private, undeveloped hardwood potentially impacted by new development, by decade to 2040 (thousand acres).*



Land cover type	2000 undeveloped land base	Area developed at density of at least one housing unit per 20 acres				Total	Percentage loss 2000 to 2040
		2000-2010	2010-2020	2020-2030	2030-2040	2000-2040	
Aspen	3	L				L	1
Montane Hardwood	2,339	92	52	73	77	294	13
Montane Riparian	75	3	2	1	1	6	8
Blue Oak Woodland	2,196	89	58	54	70	271	12
Blue Oak-Foothill Pine	685	40	21	25	17	102	15
Coastal Oak Woodland	651	12	18	15	19	63	10
Eucalyptus	4	L	L	L	L	1	23
Valley Foothill Riparian	78	4	4	3	4	15	19
Valley Oak Woodland	109	3	1	4	3	11	10

**housing density of one or more units per 20 acres; L – less than 500 acres*
Source: FRAP, 2003; FRAP 2002c

Figure 1 shows the distribution of total new ‘developed acres’ by average lot size across the whole Census split block (around 400 households) and 1990 vegetation type. For all woodlands, 84 percent of the acreage is accounted for in areas where the average lot size in the census block is between 5 and 20 acres. Only 16 percent of the acreage is within what most observers would consider development to typical subdivision level densities. This fairly sparse density class is also the best predictor for where future residential development in future decades will occur. For many ecological outcomes, it will be the private management of this mosaic rather than ‘yes/no’ decisions on new subdivisions that will be the main determinant of future ecological functionality.

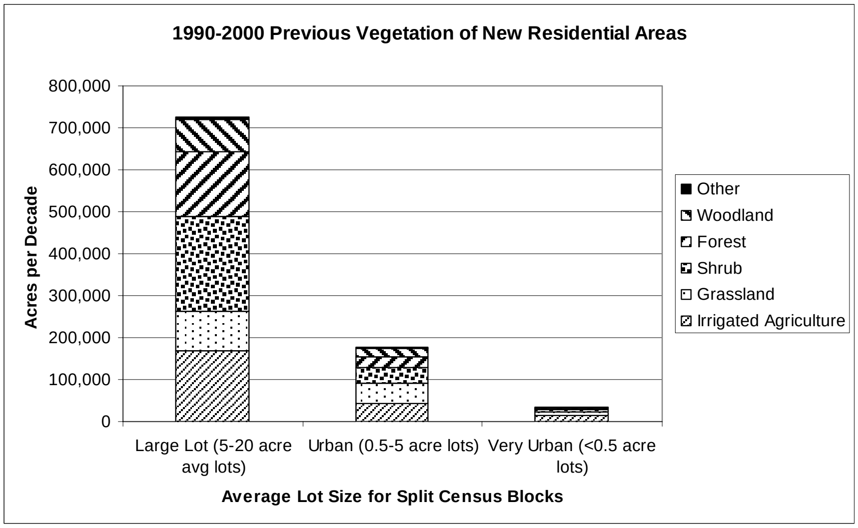


Figure 1—Size of parcels in new developed areas.

Example of Growth in the Oak Woodlands of El Dorado and Placer Counties

An analysis of the spatial pattern of residential growth in the adjacent counties in El Dorado and Placer counties just east of the rapidly growing Sacramento metropolitan region illustrates how residential conversion patterns can differ due to local policies, historical parcelization, and transportation routes.

All of the newer areas developed in 2000 are immediately adjacent to 1989 developed areas. In terms of the number of new houses (and associated tree, stand, and wildlife habitat disturbance), around two-thirds of the new houses were infill into existing developed areas and one-third was newly developed areas. Since CEQA and planning reviews may not always be used for infill projects, this suggests that much of the impact (and potential management mitigations) may not surface in formal environmental review procedures.

Table 2—*Summary table for El Dorado and Placer counties*.

Infill of	existing developed areas		new residential areas	
	El Dorado	Placer	El Dorado	Placer
Houses	3,318	7,019	1,274	5,953
Acres	112,579	110,973	48,304	43,027

A Heuristic Model of Economic Drivers of Residential Conversion

The Census-based modeling exercises of historic patterns of residential expansion provide a non-economic perspective of the probable patterns of residential development. At a regional real estate market level, however, the rate of infill will be strongly influenced by the relative real estate purchasing power of potential residents as well as market value of houses that typically have private open space values (large lots), adjacent public and private open space values, and a negative value associated with distance from major employment centers (the long commute penalty).

Many of the other papers presented at this conference focused on the habitat conservation values of public and private oak woodlands with varying levels of resource management and residential land uses. The aesthetic value of oak woodlands is also proportional to how many people can enjoy them as private or public ‘open space.’ Logically, the value will go up nearer to residential areas, even though the ecological quality may be altered with increasing residential land use and associated road and other infrastructure.

As Sunding (2005), Sunding, Swoboda, and Zilberman (2004), Wu and Plantinga (2003) have all noted, there are many overlapping and poorly understood economic policy implications between housing development and habitat conservation around metropolitan areas. The rest of this paper explores the economic drivers behind the demand for residences in the oak woodlands in the San Francisco Bay Area and the metropolitan Sacramento region.

Who Has Money to Spend on a Home in the Woodlands?

Rapid economic growth in the San Francisco Bay Area region has increased the percentage of households with high incomes compared to other parts of the state. Figure 2, based on the 2000 Census, illustrates that a larger percentage of Bay Area households have sufficient disposable income to purchase expensive homes on the periphery where most of the hardwood woodlands are. They can also relocate to areas farther from the metropolitan fringe if they want their housing investment to purchase a larger home and larger lots.

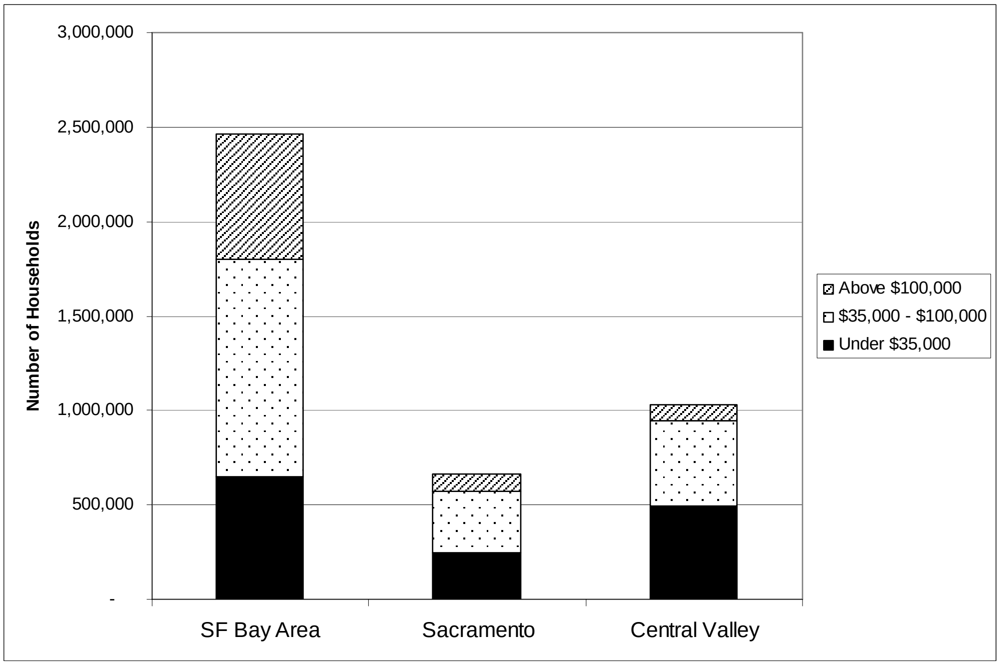


Figure 2—Number of households by 2000 incomes in three California regions.

Given the high cost of housing, households with relatively high incomes are the ones that can purchase new homes that are both larger and are on large lots or expensive houses in affluent neighborhoods nearer the desirable metropolitan centers. To look at where houses are being bought, and how much they are selling for, we used the median cost per square foot of houses sold data that is compiled by dataquick.com and published weekly in the *San Francisco Chronicle* and the *Sacramento Bee*. We chose the median cost per square foot rather than median house value to adjust for the fact that the newer houses on the periphery are typically larger. Unfortunately, Yolo County could not be included in the analysis, due a lack of house price data. Many of these growing residential areas are oak woodland landscapes.

The following figure summarizes the main patterns for the San Francisco – Sacramento double-metropolitan region. The expensive residential label refers to areas in the upper quintile of regional housing values and the inexpensive residential label refers to areas in the lowest quintile.

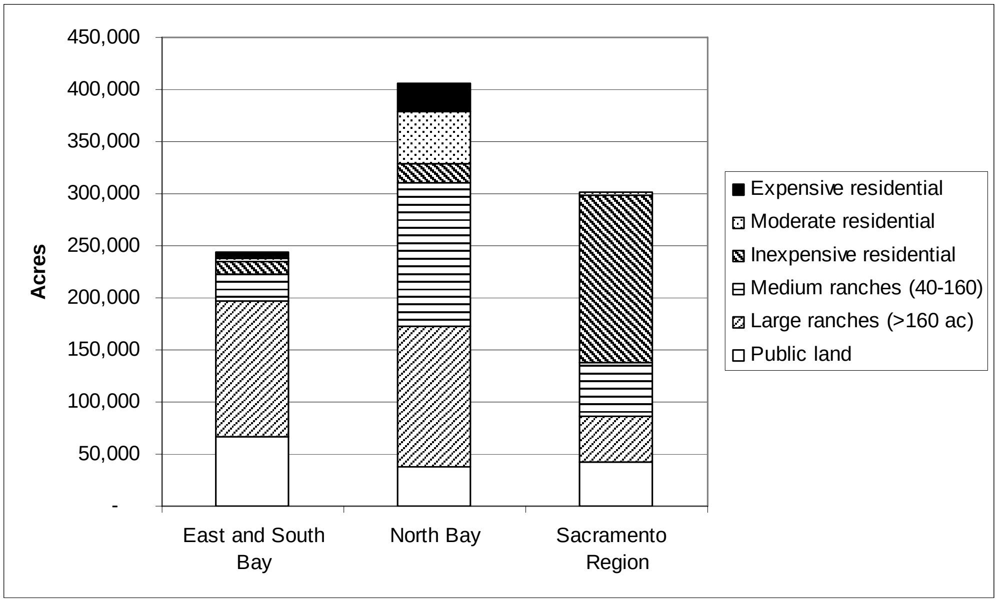


Figure 3—Hardwood land use in metropolitan Northern California.

Although the counties in the South and East Bay have the highest household incomes in the state and the region, there are relatively few acres available within a typical commute range within the hardwood areas. Compared to the two other sub-regions, a much higher percentage of hardwood lands are in public ownership or are still dominated by large ranch operations with few interspersed residences. The combination of historic public lands, locally funded land acquisitions, and private philanthropic acquisitions have combined to create one of the few areas of the state in which public open space is very large component of the hardwood lands.

The North Bay counties have slightly lower household incomes than the South and East Bay, but have considerably more acres of residential use with higher value homes in the hardwood zones. The high value of housing suggests a strong demand for open space amenities, even if the location involves a longer commute to major employment and cultural zones.

The Sacramento metropolitan region has the most area (in terms of acres and as a percentage of the total hardwood vegetation) in the current or probable residential land use zones. In addition, the housing costs are far below those registered in the greater San Francisco Bay region. One of the key inferences to be drawn from comparing the patterns among these three sub-regions on the periphery of the metropolitan areas in Northern California is that the Sacramento region will most probably capture an increasing share of the relocation, long distance commuter, Internet commuter and retiree component of residential growth.

Conclusion

The dynamics of residential expansion into the oak woodlands and other related hardwood vegetation types suggests that low density, or large lot, residential growth will dominate the acres impacted, even if it provides a relatively small portion of regional housing. More detailed analysis highlights two key insights. First, most new development within hardwood regions occurs via infill of already existing developed areas rather than via new projects. Much of this infill will still be at a relatively low density and will leave a partially altered ecological mosaic that will be quite different than either subdivisions or unfragemented lands. And second, the high cost of housing in some areas of oak woodlands will limit development only to the very affluent, but it will probably shift development pressures to other oak woodland areas in which lower housing costs make up for the greater distance from the more affluent metropolitan areas.

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Continue

Predicting the Intensity of Recreational Use of Oak Woodland Preserves[1]

Sarah E. Reed[2] and Kimberly A. Seymour[3]

Abstract

People value proximity and easy access to protected areas in urban landscapes, including state and regional parks, wildlife refuges, and open space preserves. The popularity of outdoor recreation activities such as hiking and birdwatching has more than doubled in the past 20 years, and surveys indicate that proximity to natural areas is an important factor determining where residents choose to live in California. However, the consequences of widespread recreational use in oak woodlands are largely unknown. The objectives of our study were to assess the spatial variability of recreational activity and identify site- and landscape-level correlates of recreational use of oak woodland preserves in Marin County, California. We collected two data sources to estimate the relative intensity of recreational use among 20 preserves: records of citations issued by open space rangers to recreational users and expert opinion. We used a geographic information system (GIS) database to extract several variables related to site accessibility, site amenities, and land uses surrounding each preserve. We then constructed regression models to identify which variables best predicted relative levels of recreational use for the two data sources and compared their results. Our analysis is a first step towards helping ecologists and land managers better understand variation in the intensity of recreational activity, and we make recommendations for future research on recreation impacts in oak woodlands.

Keywords: Geographic information system (GIS), oak woodlands, open space, recreation.

Introduction

Demand for outdoor recreation is growing, with unknown consequences for biodiversity and natural resources. Natural or environmental amenities – such as protected areas – are positively associated with population growth and economic development in many regions of the United States, especially the American West (Hansen and others 2002). The popularity of outdoor recreation activities – such as hiking, backpacking and birdwatching – has more than doubled in the past 20 years (Cordell and others 2005) and, in surveys, respondents articulate a growing preference for recreation opportunities in natural area parks (for example, California State Parks 2003). Contact with nature has a range of human health benefits (Frumkin 2001) and ecologists value recreation as an ecosystem service supporting human populations (Costanza and others 1997).

In California, people value proximity and easy access to protected areas, including conserved oak woodlands. Hardwood rangelands have a positive influence on property values in adjacent neighborhoods (Standiford and Scott 2002), and environmental amenities, such as parks, are important factors determining where people choose to live in California (Crump 2003). In the San Francisco Bay Area,

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[2] Postdoctoral Scholar, Department of Environmental Science, Policy and Management, University of California, Berkeley, CA 94720. email: sreed@nature.berkeley.edu.

[3] Systems analyst, David Evans and Associates, Portland, OR 97201. email: kxse@deainc.com.

surveys have shown that people prefer to travel less than 30 minutes to access a park or preserve (Bay Area Open Space Council 2004). In Marin County, for example, more than two-thirds of the protected oak woodlands land area is open for public access (*fig. 1*). Recreation is a widespread land use influencing hardwood rangelands, but its potential impacts on oak woodlands are largely unknown.

There is a growing literature on the negative impacts of recreation on plants and wildlife in a range of ecosystems. Recreation is the second-leading cause of endangerment to species on federal lands in the U.S. (Losos and others 1995) and is strongly associated with urbanization patterns (Czech and others 2000). Human recreation results in soil compaction and erosion (Liddle 1997) and reductions in vegetation height, cover and biomass (Cole 1995). In addition, recreational activity correlates with decreases in the abundance and activity levels of invertebrates (Luckenbach and Bury 1983), reptiles (Garber and Burger 1995), birds (Miller and others 1998), and mammals (Fairbanks and Tullous 2002). In a recent study in oak woodlands, we found that protected areas that permitted recreation had dramatically lower densities of mammalian carnivores than protected areas that did not permit recreation (Reed, unpublished data).

In interviews and internal reports, public agency resource managers and conservation specialists have identified documentation of the spatial and temporal variation in the types and intensity of recreational use as a critical gap in knowledge about recreation impacts and management (Gaines and others 2003). Most studies on the ecological impacts of recreation are conducted at a local scale, in a single park or preserve. However, management of human recreation occurs at a larger scale, often across multiple sites. There is likely to be spatial variation in the intensity of recreational use due to differences in accessibility and amenities among preserves. Modeling the variation of recreational use in space could help us manage recreation and better understand its potential impacts on wildlife and biodiversity in oak woodlands.

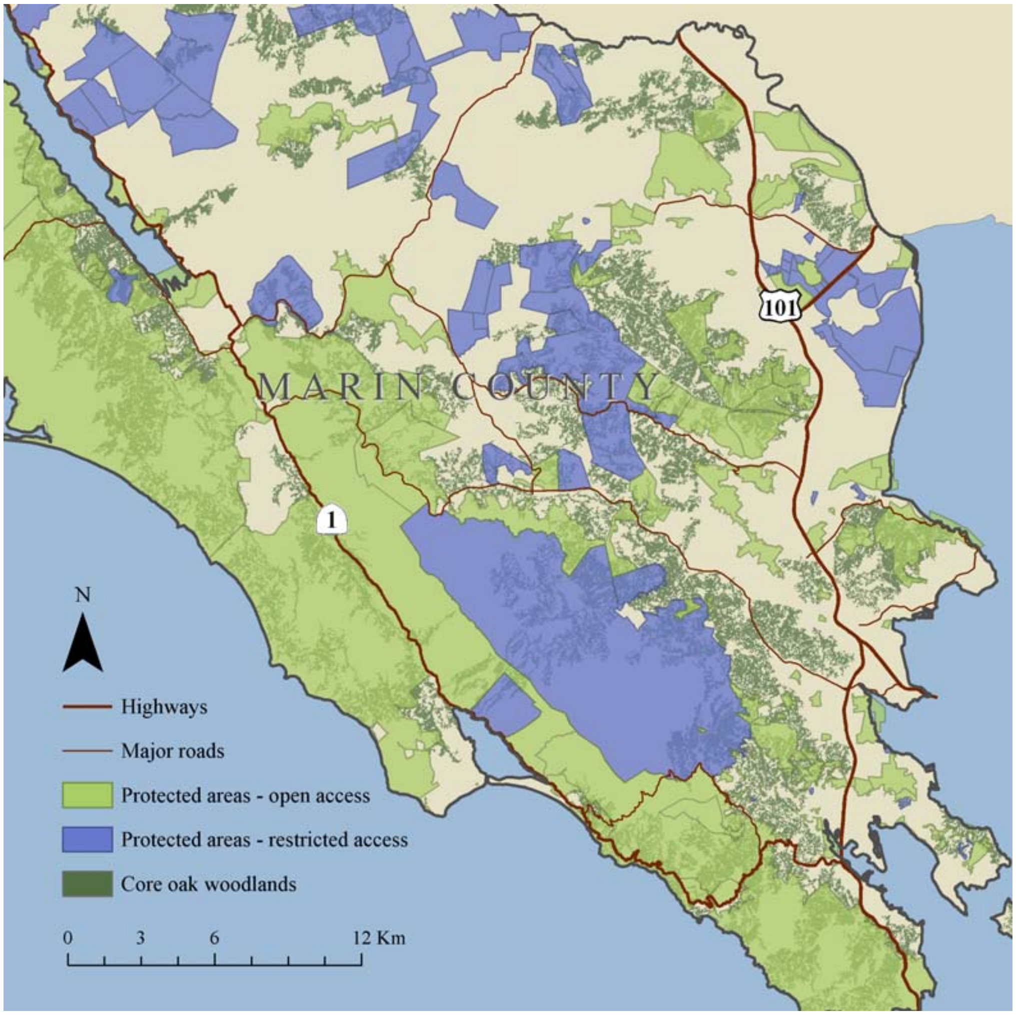

Figure 1—Public access for recreation in Marin County protected areas; 65 percent of total protected land area and 67 percent of protected land with hardwood resources is open to public access. (Source: Bay Area Open Space Council protected lands database)

The objectives of our study were to assess variability in recreational activity among preserves and to identify site- and landscape-level variables that are correlated with the intensity of recreational use of oak woodland preserves in Marin County. We collected two different data sources to estimate the relative intensity of recreational use among 20 Marin County Open Space District preserves. First, we collected records of citations issued by park rangers to recreational users and used this data as an index of the frequency of recreational visitation. Second, we constructed an expert opinion model by asking land managers to classify preserves into categories by level of use. We used a geographic information system (GIS) database to extract several variables related to site accessibility, site amenities, and land uses surrounding each preserve. We constructed regression models based on the two different data sources to select those variables that best predicted the relative intensity of recreational use among preserves and compared the results of the two models. Our analysis is a first step towards helping ecologists and land managers better understand and predict spatial variation in recreational use intensity, and we make recommendations for future research on recreation impacts in oak woodlands.

Methods

Study area

We conducted our research in Marin County, California, in hillside oak woodlands north of San Francisco Bay (38°0'N, 122°34'W). Situated between the coast and the bay, with elevations ranging between sea level and 800 m, Marin County has a range of climate conditions and vegetation, including coniferous forests, oak woodlands and grasslands, and salt marshes. Marin is densely settled along the US-101 corridor, with a total population approaching 247,000. The county also has significant natural and agricultural resources, including extensive ranch and dairy lands. With more than 57,000 ha of federal, state and county park land, Marin County is a popular recreation destination for local residents as well as visitors from the greater San Francisco Bay Area.

The Marin County Open Space District is a county-level government agency that manages 33 open space preserves, primarily located in the inland portion of the county. The preserves are managed to protect and enhance natural habitat while also providing educational and recreational opportunities for the public. We used the following criteria to select appropriate sites for our study: (1) each preserve had some habitat in oak woodland or oak savannah, (2) each preserve had marked trails or fire roads accessible for recreation, and (3) each preserve was regularly patrolled by Open Space District rangers between 2001 and 2005. The 20 open-space preserves that we selected were distributed south-north through the county and had a mean area of 207 ha (range: 13 to 649 ha; *fig. 2*).

Recreational Use Data

Ideally, we would have constructed our regression models using actual visitor counts as a response variable. However, accurate visitor counts are difficult to collect (Crompton 2001), and a detailed visitor survey was available for only one of the preserves we studied. Consequently, we examined two different data sources that provided an estimate of the relative intensity of recreational visitation among preserves. First, we collected records of citations issued by Marin County Open Space District rangers to recreational users. Because rangers patrol all of the selected sites at regular intervals, visiting each trail and fire road a minimum of two times each year (B. Sanford, personal communication), we assumed that the number of citations issued was proportional to the number of recreational visitors to each preserve.

To minimize any effects of seasonal or annual variability, we summarized records of citations collected over five years, between 2001 and 2005. Marin County Open Space District rangers issued a mean of 50.6 (range: 1 to 202) citations in each preserve during this period. Of these citations, a mean of 41 percent were issued for dog-related infractions, 9 percent for bike infractions, 3 percent for motor vehicle infractions, and 46 percent for other infractions. We pooled total citations in each preserve for all years for our regression analyses.

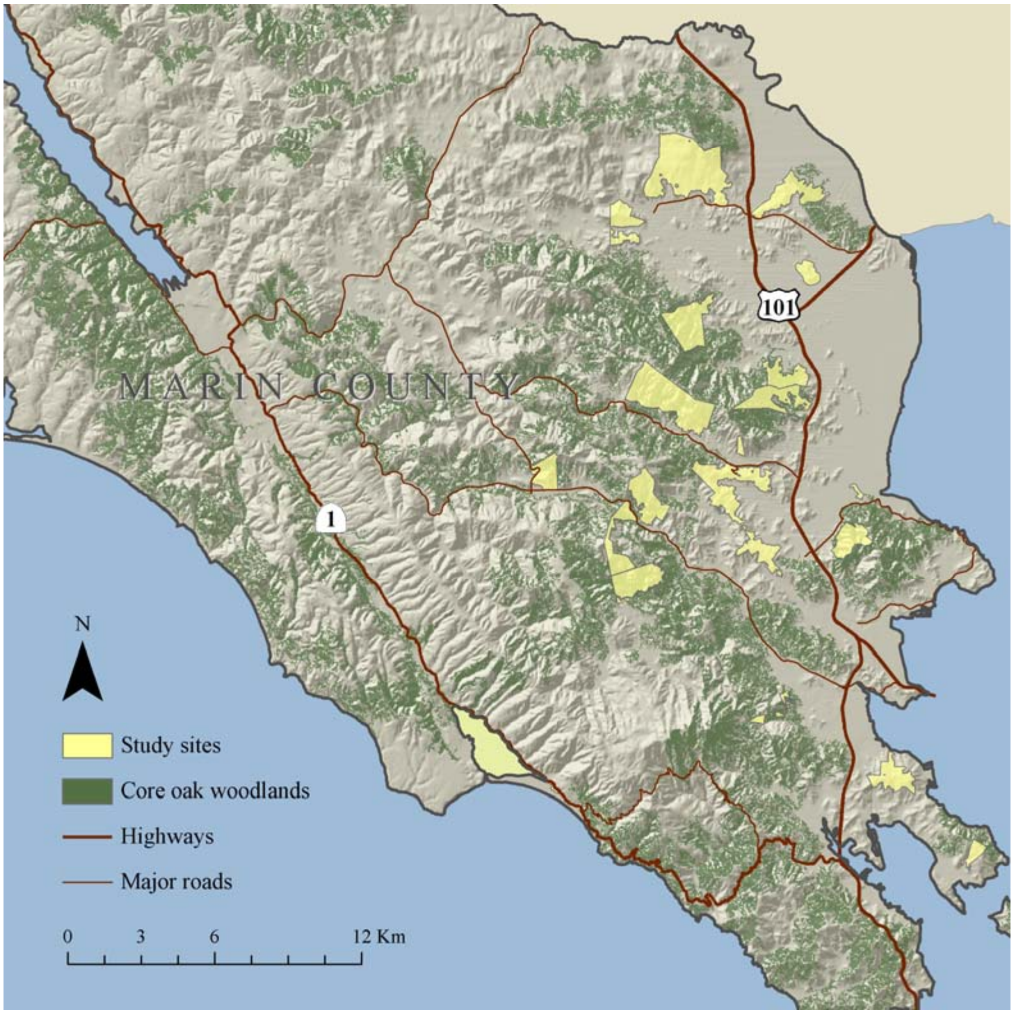

Figure 2—Locations of 20 study sites and core oak woodlands in Marin County, California.

Expert opinion provided our second source of data on recreational use of the preserves. We asked the District's head ranger to classify the 20 preserves into categories representing their relative visitation rates. The head ranger classified the preserves into three levels of use (low, medium and high), and these classifications were verified by the district's superintendent. Overall, 5 of the 20 preserves were classified as low-, 8 as medium-, and 7 as high-use.

Site and Landscape Attributes

We collected and extracted 15 site- and landscape-level variables for development of our model (*table 1*). We referred to prior studies on recreational visitation (for example, Termansen and others 2006) as well as our own knowledge of the study system to identify potential predictor variables. The Marin County Open Space District provided us with GIS data on preserve boundaries, fire roads, and trails. We used these data to calculate the area, total trail and fire road distance, and trail and fire road density (distance per unit area) for each preserve. We used preserve maps to count the number of marked entrance gates at each site. We used GIS data provided by the North Coast Integrated Hardwood Range Management Program to calculate topography and land cover variables for each site. We used a 30 m digital elevation model (DEM) for Marin County to calculate the mean and range of elevations and slope for each preserve. We used CalVeg vegetation data for Marin County to calculate proportions of each site in herbaceous and hardwood land cover. We used Google Maps (http://maps.google.com) to calculate driving distances and driving times to each preserve. We assumed that most non-local recreational users would be traveling via US-101 to access the preserves, and we calculated driving distances and times from US-101 to the nearest entrance gate at each preserve. We used a digitized parcel map for Marin County to calculate the number and sizes of land parcels located within 500 m of each preserve's boundary. We calculated the number of suburban (0.04 to 0.4 ha), exurban (0.4 to 8 ha), and rural (> 8 ha) parcels adjacent to each preserve, as well as the total number of parcels. All GIS analyses were conducted in ArcGIS 9 (ESRI, Redlands, CA, USA).

Statistical Analyses

We used JMP 6 (SAS, Cary, NC, USA) to conduct all statistical analyses. We transformed all predictor variables to meet assumptions of normality for regressions (*table 1*). We began by exploring the relationships of each predictor variable with our two response variables. We used linear regressions to explore relationships between predictor variables and total citations and ordinal logistic regressions to explore relationships between predictor variables and level of use. We coded preserves with low levels of recreational use as a value of one, medium as two and high as three, so that positive parameter values in ordinal logistic regressions would correspond to increasing levels of use. We then tested for correlations among the predictor variables. To select a final model for each data source, we limited our analysis to predictor variables that were independent of one another ($r < 0.7$). We included only the predictor variable from each pair or group of related variables (for example, driving distance to US-101 and driving time to US-101) that had the strongest correlation with the recreational use data. We used a mixed, stepwise variable selection process to select the best, most parsimonious model for each response variable. We selected a final multiple linear regression model for the citations data and a final multiple ordinal logistic regression model for the expert opinion data.

Table 1—*Site and landscape attributes collected for model development. Data codes and transformations are indicated for each variable.*

Site and landscape attributes	Code	Transformation
Site area	AREA	$x^{1/3}$
Number of entrance gates	GATES	$x^{1/3}$
Trail and fire road distance	TF_DIST	$x^{1/2}$
Trail and fire road density	TF_DENS	None
Mean elevation	ELEV_MEAN	None
Elevation range	ELEV_RNG	None
Mean slope	SLOPE	x^2
Proportion of site in herbaceous land cover	P_HEB	None
Proportion of site in hardwood land cover	P_HWD	None
Driving distance to US-101	101_DIST	$\mathrm{Log}(x)$
Driving time to US-101	101_TIME	$x^{1/3}$
Number of suburban parcels within 500m of site boundary	SUB_500	$x^{1/2}$
Number of exurban parcels within 500m of site boundary	EX_500	$x^{1/3}$
Number of rural parcels within 500m of site boundary	RUR_500	$x^{1/2}$
Total number of parcels within 500m of site boundary	TOT_500	$x^{1/3}$

Results

Our exploratory data analyses revealed that several site- and landscape-level attributes were significantly (p<0.10) correlated with each of the recreational use data sources (*table 2*). Site area, the number of entrance gates, trail and fire road distance, and the numbers of adjacent parcels for all size classes (suburban, exurban, rural and total) had significant, positive correlations with the total number of citations issued in each preserve. Mean slope had a significant, negative correlation with total citations. We did not find significant relationships between trail and fire road density, elevation, land cover or driving distance or driving time from US-101 and total citations issued. For the expert opinion data, we found significant, positive correlations between trail and fire road distance, trail and fire road density and the number of adjacent exurban parcels and the level of recreational use. We did not find significant correlations for the remainder of the variables.

Table 2—*Exploratory data analysis. Parameter estimates and model fit statistics are given for linear regressions of site and landscape variables versus total citations issued and for ordinal logistic regressions of site and landscape variables versus level of use. Bold typeface indicates correlations significant at the level* p*<0.10.*

	Total citations		**Level of use**	
Predictor variable	**Parameter estimate**	**R^2**	**Parameter estimate**	**R^2**
AREA	**0.485**	**0.31**	2.58E-03	0.02
GATES	**2.94**	**0.71**	0.0983	0.03
TF_DIST	**0.0176**	**0.23**	**0.362**	**0.24**
TF_DENS	3.90E-03	0.00	**0.0515**	**0.11**
ELEV_MEAN	-1.16E-03	0.00	-1.16E-03	0.00
ELEV_RNG	3.44E-04	0.00	1.74E-06	0.00
SLOPE	**-3.78E-03**	**0.18**	-0.0395	0.01
P_HEB	1.10	0.06	0.277	0.00
P_HWD	-1.40	0.11	-0.0176	0.00
101_DIST	-0.375	0.08	-7.19E-04	0.00
101_TIME	-0.660	0.07	-9.83E-03	0.00
SUB_500	**0.0564**	**0.35**	9.75E-04	0.07
EX_500	**0.836**	**0.34**	**0.0176**	**0.11**
RUR_500	**0.678**	**0.21**	0.0591	0.03
TOT_500	**0.274**	**0.34**	1.01E-03	0.08

Our mixed, stepwise selection process yielded a multiple linear regression model for the citations data that included three significant ($p<0.05$) predictor variables (*table 3*). Trail and fire road distance and the total number of adjacent parcels were positively related to recreational use intensity, while mean slope was negatively related. This final model explained 66 percent (R^2 adjusted) of the variation in the citations data. Our model selection process for the expert opinion data yielded a multiple ordinal logistic regression model that included two significant ($p<0.05$) predictor variables (*table 4*). Trail and fire road distance was positively related to level of recreational use, while elevation range was negatively related to the level of recreational use. This final model explained 36 percent (R^2 adjusted) of the variation in the expert opinion data.

Table 3—*Multiple linear regression model of site and landscape correlates of total citations issued. All predictor variables selected in the final model are statistically significant at p<0.05. The adjusted R^2 value for the whole model is 0.66.*

Model term	**Parameter estimate**	**SE**	***P***
TF_DIST	0.0157	0.0056	0.02
TOT_500	0.231	0.071	0.01
SLOPE	-0.00472	0.00131	< 0.01

Table 4—*Multiple ordinal logistic regression model of site and landscape correlates of level of use. All predictor variables selected in the final model are statistically significant at* $p<0.05$. *The adjusted* R^2 *value for the whole model is 0.36.*

Model term	**Parameter estimate**	**SE**	***P***
TF_DIST	6.06E-04	2.32E-04	< 0.001
ELEV_RNG	-9.56E-03	5.03E-03	0.02

Discussion

The citations and expert opinion data we collected indicate that there is considerable variability in the level of recreational activity among Marin County Open Space District preserves. In addition, we found a high degree of overlap in the predictor variables selected in final multiple regression models for the two data sources. The concurrence between the models indicates that site attributes are the strongest predictors of recreational visitation to oak woodlands. Although the parameter values are not directly comparable, due to the different modeling approaches, both models indicated a significant, positive relationship between trail and fire road distance and the intensity of recreational use. This result suggests that networks of trails for hiking, biking, and horseback riding are attractants for recreational visitors. Both models also indicated that topography may influence the intensity of recreational use. The citations data model showed a significant, negative relationship between mean slope and total citations issued, whereas, the expert opinion model showed a significant, negative relationship between elevation range and level of use. Mean slope and elevation range were positively correlated (R^2=0.41), and negative relationships with these variables suggest that preserves with steeper topography may be less desirable for recreational visitors.

Previous studies in other ecosystems have found that driving distance or travel time from human population centers is a significant predictor of the rate of recreational visitation to parks or forest preserves (Hill and Courtney 2006, Ode and Fry 2006). In our study, we found no significant correlations between either driving time or driving distance to US-101 and either response variable. For the citations data model, we found a significant, positive relationship with adjacent parcel density, implying that local populations, rather than destination visitors, may be the primary users of Marin County Open Space preserves. However, this result was not confirmed by the expert opinion model, and it is possible that adjacent human population density could correlate with increasing numbers of complaints and, subsequently, increasing numbers of citations. In addition, our approach assumed that regional visitors would travel to the sites from US-101. A combined approach, incorporating human population density in different travel 'time zones' from each preserve (for example, Hill and Courtney 2006), could clarify the relationships between travel distance, population density and recreational visitation.

Our results were consistent with other studies that have found various site attributes and amenities—including forest type and terrain (Termansen and others 2006), parking availability (Hill and Courtney 2006), and length of available trails (Ode and Fry 2006)—were important determinants of recreational visitation. Our finding that mean slope or elevation range had a negative influence on recreational visitation contrasts with studies of recreation in other habitats, which have found that visitors prefer undulating rather than flat terrain (Termansen and others 2006). However, hillsides in oak woodlands can be quite steep—mean slopes in the preserves in our study ranged over 25 degrees – and it seems reasonable to assume that visitors to Marin County preferred sites with more moderate terrain. We did not find a significant relationship between land cover type and the intensity of recreation use, although opposing trends with hardwood and herbaceous cover in the linear regressions (*table 2*) indicate that visitors may have a slight preference for open rather than densely forested oak woodlands.

Conclusion

Human recreation is a widespread land use affecting oak woodlands in Marin County (*fig. 1*) and throughout California. A growing body of literature indicates that ecosystems are impacted by both the intensity (for example, Garber and Burger 1995) and spatial extent (for example, Fairbanks and Tullous 2002) of recreational activity. Some factors affecting recreational visitation, such as trail networks, could be influenced by management actions in individual parks or preserves. Other site-level attributes, such as topography, could be taken into account in regional conservation and recreation planning processes. Overall, GIS-based models of recreational visitation, such as those described here, could be useful tools for evaluating trade-offs in land management and acquisition decisions.

The primary limitation of this study was the quality of the data we used to estimate relative levels of recreational activity among preserves. The advantages of the citations data were that it was continuous and collected over a period of five years; however, the relationship between the citations rate and recreational visitation is unknown and the data could be biased by uneven patrol effort or disproportionate citation rates among preserves. The expert opinion data was likely to be relatively accurate, but the small number of ordinal categories provided less power to detect variable relationships. In conclusion, we recommend collecting actual visitor count data to validate the results of model analyses. Accurate and replicated visitor count data can be challenging to collect (Crompton 2001), but is a critical limitation for most multi-site studies of recreation use (for example, Ode and Fry 2006). Collecting such data would clearly improve the predictive power and accuracy, as well as the applicability, of spatial models. In addition, pairing visitor counts with surveys for biodiversity could help us better understand the ecological impacts of recreation in oak woodlands and other habitats. Our study is a first step towards understanding the effects of growing demand for recreation on oak woodlands in Northern California. Ultimately, we hope the results of this and future research efforts can help park managers anticipate the relative intensity of recreational use and mitigate potential impacts to wildlife and biodiversity.

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Continue

Determining Significance Within CEQA: A New UC Program to Assist Planners in Conserving Oak Woodlands[1]

Gregory A. Giusti[2] and Douglas D. McCreary[3]

Abstract

In 2004, the California State Legislature passed Senate Bill 1334 (Bill), titled *Oak Woodlands Conservation: Environmental Quality*. This Bill states, "A county…shall determine whether a project within its jurisdiction may result in a conversion of oak woodlands that will have a significant effect on the environment". Once a determination has been made, counties have the option to 1) evaluate the utility of conservation easements as a vehicle for conservation; 2) enforce mitigation planting; 3) make a in-lieu contribution to the Oak Woodlands Conservation Fund (established in 2001 under the administration of the Wildlife Conservation Board), or implement other mitigation actions as outlined by the county. This Bill initiates a new attitude for the state that requires all counties to consider significant impacts as defined in the California Environmental Quality Act (CEQA) for all non-agricultural projects affecting oaks.

Faced with implementing this Bill, counties began asking the University of California (UC), the California Department of Fish and Game (DFG), the California Department of Forestry and Fire Protection (CDF) and the Wildlife Conservation Board (WCB) questions, including what types of projects fell under the purview of the Bill, what constituted "significant impacts," and how to determine suitable, appropriate mitigation. To help answer these questions, the UC Integrated Hardwood Range Management Program (IHRMP) initiated a grant proposal to the WCB that was funded in early 2006. The grant proposed activities and products to specifically assist planners who are charged with implementing SB 1334 at a local level.

In response to the county questions, the agencies receiving inquiries about SB 1334 formed a committee to develop and disseminate information, including compliance guidelines and effective strategies to conserve oak woodlands. Specifically this committee charged itself with developing a strategy and tools that planners could use to analyze proposed project effects on oak woodlands. This new initiative includes both static and interactive Web-based decision keys, PowerPoint presentations, and visual comparison standards for assessing oak woodland impacts. Although these efforts are ongoing, the products will be important tools to help counties comply with SB 1334 and conserve their important oak woodlands.

Keywords: CEQA, Planning, Matrix.

Introduction

California continues to experience population growth and expansion into areas traditionally used for extensive and intensive agricultural operations. This growth is

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[1] An abbreviated version of the paper was presented at the Sixth California Oak Symposium: Today's Challenges, Tomorrow's Opportunities, October 9-12, 2006, Rohnert Park, California.

[2] North Coast Area Hardwoods Advisor, Mendocino County UCCE, 890 N. Bush Street, UCCE-Mendocino County, Ukiah, CA 95482.

[3] IHRMP and Area Natural Resources Specialist, Integrated Hardwood Range Management Program, 8279 Scott Forbes, Browns Valley, CA 95918.

proving to be challenging rural county planning departments as they try and grapple with issues and subjects never before confronted regarding growth impacts to native oak forest systems (Giusti and others 2005). Though some level of growth and sprawl is ubiquitous throughout the state the regions witnessing the greatest increases include the Central Valley, Sierra foothills and Central Coast.

Oak removal can certainly have significant impacts on environmental quality (Johnson 1998; Merenlender and others 1998). Jurisdictions have used various planning vehicles and approaches to try and achieve oak conservation goals, including general plan language, zoning restrictions, tree protection ordinances, heritage tree recognition programs, and programs that support the purchase and development of conservation easements.

Until recently, counties have independently developed these policies and procedures to address development impacts to oak woodlands without clear direction from state resource agencies (Harris and Kocher 2002, Giusti and others 2005). This condition changed abruptly with the passage of SB 1334 (Kuehl, 2004) when the Legislature mandated that counties assess significant impacts as defined in CEQA to oaks in non-agricultural projects.

Previous to the passage of SB 1334 the state of California’s position towards oak woodlands, as defined and administered by the California State Board of Forestry and Fire Protection, was that counties should develop and implement oak conservation policies that they felt appropriate (Giusti and Merenlender 2002). Consequently, the state has maintained a position that oaks would not be regulated in a similar fashion as conifer species, thereby deferring to counties to define and develop appropriate measures to insure oak woodland conservation.

SB 1334 represents a dramatic change in policy direction by mandating counties to comply with CEQA when significant impacts to oaks are identified. This shift has resulted in many requests for information from county planners, developers, home owners and others for help in understanding both the implicit and explicit implications of this bill. There is no question this legislative act has forced people to think about project impacts and subsequent effects on oak woodlands in terms never before considered. Additionally, it has pressed resource agencies and institutions toward a direction of providing information to help delineate the ambiguous terms and definitions as currently provided in CEQA.

UC’s Approach to Providing Guidance to This Issue

The University of California’s Integrated Hardwood Range Management Program (IHRMP) requested grant support from the Wildlife Conservation Board to develop a new program and source of information and educational materials to help planners implement this bill. The grant was awarded in February 2006. Following the grant award, an interdisciplinary team was assembled and included inter-disciplinary resource professionals from the WCB, CDF, FRAP, CDFG, and UC to outline a program that would provide a performance-based, rather than prescriptive-based, approach to oak woodland conservation in order to try and avoid the “institutionalized,” rigid system currently in place for timber harvest practices.

There was consensus among committee members that county planners need access to science-based information that allows them to develop spatially explicit planning scenarios in the early stages of the development process. This is consistent with the recommendations made by Forman and Collinge (1997) who maintained that in order to conserve biological diversity, a crucial time for spatially derived planning is when the first 10 to 40 percent of the natural vegetation is altered or removed from the landscape. Furthermore, it was recognized that given the variety of regional situations that face county planners, it is important to first provide broad, conceptual conservation goals and then develop applicable tools that allow the concepts to be visualized "on the ground."

Further guidance to the issue is provided by the Ecological Society of America (ESA) (Dale and others 2000) who developed a basis for conservation planning that captures the conceptual approach to planning that the committee supports. In their Land Use Committee Guidelines for Land Use Planning and Management, the ESA recommends:

1) Examine the impacts of local decisions in a regional context;
2) Plan for long-term change and unexpected events;
3) Preserve rare landscape elements and associated species;
4) Avoid land uses that deplete natural resources over a broad area;
5) Retain large contiguous or connected areas that contain critical habitats;
6) Minimize the introduction and spread of non-native species
7) Avoid or compensate for effects of development on ecological processes; and
8) Implement land use and land management practices that are compatible with the natural potential of the area.

There was further consensus on the recognition of the chasm that exists between conceptual design and pragmatic implementation in the politically charged arena of county planning. It is clear that in order to have scientifically validated approaches included in the planning process requires the development of concise, well-articulated decision-making tools specific for oak woodlands. Those tools would strive to incorporate the current conventional wisdom pervasive throughout the literature that identifies those elements or characteristics most important for maintaining the integrity of oak woodlands (i.e., old trees/forests, maintaining rare and representative habitats, riparian corridors, water quality and quantity, ecosystem functions and natural connectivity). Additionally, any planning tools should strive to assist planners in promoting compatible land uses to avoid or minimize fragmentation whenever possible.

Finally, the question of "*What is Significant?*" has to be addressed if planners are to have any real chance to influence the direction and impacts of a proposed project. Rossouw (2003) suggests that *Impact Predictions* be based on measurable attributes that can be quantified or qualified based on the long-term nature of the change being proposed. In most cases, predictions of the impacts can be conceptually developed under the subject headings of:

- Spatial extent;
- Duration of the impact;
- Intensity or severity of the impact;
- Status of the impact (i.e., either positive (a benefit) or negative (a cost), or neutral);

- Reversibility (i.e., reversible or permanent);
- Degree of certainty; and
- Mitigatory potential.

A Work in Progress—Web-Based Technology

Technology is allowing scientist and non-scientists to collect scientific data and disseminate the results broadly. For example, an interactive Web-based program is already an important component in the detection and tracking of Sudden Oak Death (www.suddenoakdeath.org) in California. The ability for people to communicate via e-mail and similar technologies provides a readily available tool for planners to exchange questions, ideas and sources of information if an organization or institution is willing to serve as the catalyst to support the system. Part of the grant agreement with WCB is to have the IHRMP develop and support an interactive, Web-based communication tool for planners. The design is to use the IHRMP home page as a portal allowing planner's access to:

1. A bulletin board to post pertinent oak-related planning questions and or information for broad dissemination to a non-specified audience seeking reference materials, sources of information, contact information, etc.
2. A collaborative tool system wherein planners who register can participate in a "working group" Web experience allowing for oak-related discussions among resource professionals, planners, agency personnel, who are struggling with oak/planning specific situations.
3. Easy access to FRAP-generated county oak woodland maps,
4. Links to species accounts for common California oaks,
5. Power Point presentation providing background information and explanations to a planner's obligations under SB 1334.

Field and Office Decision Tools

Ecological resource decisions should be derived from field observations, literature research and data collection. The challenge for planners is to meld the instructions and guidance provided for by science with the intensity of the politically driven planning process. The determination of "significance" as defined in CEQA is at the core of implementing SB 1334. That decision will guide both the financial costs and the political intensity associated with the project. Providing sound, science-based information into the decision-making process is crucial for the well-being of both the individuals and the oak woodlands involved in the discussion. A decision matrix has been drafted that should ultimately assist planners in classifying the condition of the oak woodlands under discussion.

The matrix relies on using a set of criteria as a means to qualitatively establish rudimentary thresholds of significance to first broadly define impacts in simple terms. These criteria simply apply subjective reasoning to first determine the level of impact being proposed (*table 1*).

Table 1—*Categories for the rating of impact magnitude and significance (adapted from Rossouw 2003).*

Impact Magnitude and Significance Rating	
High	Of the highest order possible within the bounds of impacts that could occur. In the case of adverse impacts, there is no possible mitigation that could offset the impact, or mitigation is difficult, expensive, time consuming or some combination of these. Examples include conversion of oak woodlands; large-scale projects impacting a large number of trees or acres; projects that result in causing or exasperating fragmentation issues.
Medium	Impact is real but not substantial in relation to other impacts that might take effect within the bounds of those that could occur. In the case of adverse impacts, mitigation is both feasible and fairly easily possible. Examples include oak trees or acreage already within the boundaries of an existing development; projects that can be adjusted to easily minimize the negative impacts to oak resources.
Low	Impact is of a low order and therefore likely to have little real ecological effect. In the case of adverse impacts, mitigation is either easily achieved or little will be required, or both. Examples include removal of a few number of trees from a residence; pruning or shaping activities on existing oaks.
No impact	Zero impact

This approach allows both the planner and the applicant to make a relatively straight-forward and economically cost-effective assessment of where the project may lie in regards to environmental impacts and potential mitigatory actions and associated costs.

Furthermore, a rating system for impacts recognizes that each project site has a peculiar history and situation whereby the history of land-use practices at any particular site may offer a different set of variable planning scenarios from which to start the discussion. It further recognizes the variability between properties whose qualities can range from a wildland state to properties whose oak characteristics have been obliterated. The rating system strives to establish a baseline from which to initiate the decision-making process.

To further assist in the evaluation process, the matrix is designed to guide a planner through a series of conditions to ascertain if the site represents an oak woodland whose ecological functions are still relatively “intact,” “moderately degraded,” or “severely degraded.” This relative comparison is intended to classify the current state of the site in order to establish a baseline from which to determine both significance and appropriate mitigation considerations.

Inherent in this approach is the realization that some core oak woodland acres are considered more ecologically important than others and attempts to have the planning process recognize this condition. Once the site condition has been determined, then the proposed project impacts can be fully gauged and the potential impacts determined. The condition description accepts that any evaluation must address more than simply the impacts to the trees; the planner should consider the potential impacts to the other tangible aspects of the woodland.

The second step, following the initial qualitative assessment of thresholds previously described, in the matrix poses the question; is the site?

Intact?

An "intact" woodland is a site is currently in a "wild state" being managed for grazing, open space, recreation, etc., wherein all of the ecological services are still being provided (i.e., shade, groundwater filtration, wildlife/fish habitat, nutrient cycling, wind/noise/dust abatement, etc). In this condition, roads and stream crossings are absent or minimal over vast portions of the site. Trees, both dead and alive, dominate the landscape and the site is capable of natural regeneration of oaks and other plant species. The site is absent of any development that would inhibit the movement of wildlife, and the existing development is limited to a small number of residences with service buildings or barns. This site is recognized as *Intact Woodland wherein alterations to the existing condition should be considered significant and unavoidable.* Examples include large- to moderate-sized (>1,000 acres) private ranches, expansive oak woodlands, zones for agriculture, open space, scenic corridors.

Moderately Degraded?

A "moderately degraded" site has obviously been altered from a pristine or wild state condition. It is currently a state in which oak trees are present; natural regeneration is capable of occurring; limited ecological services are still being provided; and the site still provides for utilization by wildlife and possibility fish. Roads and stream crossings are present but limited or clustered. Developed areas are centralized and concentrated over a small percentage of the site. The site is recognized as a *Moderately Degraded Woodland wherein alterations to the existing condition should be considered significant but mitigable*. Mitigation measures may diminish the environmental impacts to achieve no further degradation of the site. Examples may include some golf courses; large ranches that have been subdivided into large parcels (>100 acres); and oak woodland subdivisions that share "common grounds" of intact woodland acres.

Severely Degraded?

A "severely degraded" site has been dramatically altered from a pristine state and is currently in a condition that has no trees or very few old decadent residuals. It is being managed in such a way that natural regeneration is not possible or impractical; the soil is compacted or contaminated; and/or has been developed for residential, commercial or industrial purposes. Roads and stream crossings are commonplace, and fencing and other obstructions limit wildlife access and movement. Alternations to this site description may be considered *less than significant* if the loss of a single or a few number of trees does not dramatically alter the surrounding condition.

Once the threshold impacts and site class have been determined, a paired comparison allows for a more certain assessment of the proposed project and its relevance to the issue of significance. For instance, a project of likely "high impact" proposed for an "intact" woodland would be viewed as significant under CEQA; or, a project of likely high or moderate impact on a "slightly altered" oak woodland may well be considered "significant" under CEQA guidelines. Conversely, a project proposing to remove one or very few trees from a highly urbanized site may indeed not be determined significant. This assessment must address more than simply the impacts to the trees; the planner should consider the potential impacts to the other tangible aspects of the woodland.

To further support the decision-making process, a field assessment tool is being developed to quickly determine 1) the condition of the site, 2) the ecological functions that may be impacted by the proposed project, and 3) the criteria and elements that should be considered for mitigation.

Educational Support and Outreach

The UC IHRMP has provided educational leadership in the subject of oak woodlands since 1985. That role will only be enhanced through this new initiative as the program strives to develop progressive and innovative approaches to problem solving. Coupled with the newly developed materials and delivery methods, the program has recently updated the *Planner's Guide to Oak Woodlands* (Giusti and others 2005) which delivers a broad array of subject matter useful as a reference tool for the ecology and conservation of oaks. Additionally, the program has developed a planning White Paper (Giusti and others 2004) designed to assist broad audiences with the challenges facing California regarding the conservation of oaks and biological diversity.

Concurrent with these visual resources, the program continues to organize regional workshops and the Oak Research Science Symposium to convey new information and technologies.

Discussion

SB 1334 is serving as a catalyst to prompt new and innovative approaches to determining significance within CEQA in ways never before attempted. The Bill maintains the state's long-held attitude that local governments should implement oak conservation policies.

There is little controversy that land-use practices can have various impacts on oak ecosystems, their habitats and dependent species (Merenlender and others 2005). The combined affects of land use practices can have long-term impacts on the functions and processes necessary to sustain oak ecosystems over time. The ability of the planning process and the importance that planners play in recognizing and minimizing the ecological effects of fragmentation in a rapidly urbanizing state can not be overstated.

This newly introduced program represents an innovative and unprecedented approach to environmental assessment and impact determination, based on the most current scientific literature that addresses the role of planning in the conservation of trees and biological diversity of forest systems (Foley and others 2005, Lee and others 2006, Manning and others 2006, Seiver and Hatfield 2001, Rossouw 2003). Further, it represents a divergence from past, prescriptive regulatory approaches legislated to other forest types and scenarios. This approach attempts to guide a planner and project applicant through a process by which significance can be determined on the basis of the relative starting condition of the site. Furthermore, it attempts to establish a performance-based approach to a highly charged political planning system that is adverse to the precedent established under the current timberland regulatory system.

The strategy described here is designed to be used in combination with other planning tools and programs to support a county's desire to conserve oak resources. In addition, resource maps will always be necessary to examine the extent and ownership patterns of oak woodlands. Other policies that provide guidance and leadership within a county's jurisdiction may also affect the decision-making process; such as, general plans and county oak management plans. This system is designed to be a component of a comprehensive, county-wide oak management plan, or policy that is included in the appropriate planning document (e.g., General Plan). The combination of such tools is vital if a professional is to have the necessary tools available to transform their traditional planning approaches into progressive, ecologically based conservation tools (Environ. Law Institute 2003).

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Continue

Sudden Oak Death I

Continue

Woodland Structure Affects Intensity of Infection by an Exotic Forest Pathogen[1]

Nathan Rank,[2] Hall Cushman,[2] and Ross Meentemeyer[3]

Abstract

Woodland ecosystems often consist of a mosaic of interacting dominant woody species that vary in density and abundance. Local variation in dominant species abundance may influence spread of plant pathogens across this heterogeneous landscape. We investigated this possibility in a 275 km2 study area in eastern Sonoma County, which is being invaded by the pathogen that causes Sudden Oak Death, *Phytophthora ramorum*. We assessed symptoms of infection by *P. ramorum* of foliar and canker hosts in 2004 and 2005 in 202 randomly located plots. Our results showed that the widespread foliar host, bay laurel (*Umbellaria californica*), exhibited symptoms of disease throughout the study area, while canker hosts showed no signs of infection in most plots. This suggests that SOD spread among foliar hosts much more rapidly than from foliar hosts to canker hosts. With the high precipitation over the past two rainy seasons, we expect the disease to progress into canker hosts over the next several years. We also found that density of bay stems and degree of infection on bay laurel depended partly on presence of oak species. For example, the proportion of bay stems with symptoms of *P. ramorum* was 18% greater when coast live oak (*Quercus agrifolia*) was present than when it was absent. Coast live oak presence was also related to number of symptomatic bay leaves per tree. We suspect that our findings arise from the fact that the pathogen spreads most rapidly in stands where few canker host individuals inhibit dispersal among foliar host trees. Although previous studies have shown that abundance of bay laurel is related to infection levels in oaks, this is the first study that we know of suggesting that the presence of canker hosts affects infection levels on bay laurel, the main foliar host of *P. ramorum*.

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[2] Professor and Assoc. Professor, Sonoma State University, Department of Biology, Department of Biology, 1801 E. Cotati Avenue , Rohnert Park, CA 94928. rank@sonoma.edu and cushman@sonoma.edu

[3] Assoc. Professor, Director of the Center for University of North Carolina-Charlotte, 9201 University City Blvd., Charlotte, NC 28223. e-mail: rkmeente@email.uncc.edu

Continue

Consequences of *Phytophthora ramorum* Infection in Coast Live Oaks[1]

Brice A. McPherson,[2] David L. Wood,[3] Sylvia R. Mori,[4] Pavel Svihra,[5] Richard B. Standiford,[2] and N. Maggi Kelly[6]

Abstract

Sudden oak death, caused by *Phytophthora ramorum*, has infected and killed large numbers of oaks (*Quercus* spp.) and tanoaks (*Lithocarpus densiflorus*) in California since the mid 1990s. Since March 2000 we have been investigating the interactions between patterns of disease progression and broader landscape-scale patterns of disease incidence and expansion in study plots in Marin County. The incidence of new infections has continued to increase in both coast live oaks (*Q. agrifolia*) and California black oaks (*Q. kelloggii*), and very rapidly in tanoaks. The net result of more than10 years of *P. ramorum* presence in these forests has led to dramatically altered overstory structure. Larger diameter trees are more likely to be infected and once infected, are more likely to be attacked by beetles. Beetle attacks dramatically lowered the estimated median survival of infected coast live oaks, from 7 years to less than 3 years, with comparable results for tanoaks. In 2001 we established landscape-scale monitoring in Marin and Santa Cruz Cos. to assess spatial and temporal dynamics of disease spread within vegetatively heterogeneous forests. In Marin Co., the proportion of coast live oaks that was infected decreased by 2004, while the proportions increased in tanoaks and Shreve oaks (*Q. parvula* var. *Shrevei*) in Santa Cruz Co. by 2005. To evaluate the role of bark and ambrosia beetles associated with this disease in coast live oaks, we inoculated asymptomatic trees with *P. ramorum*, used an insecticide to experimentally prevent beetle attacks, and placed traps on inoculated and wounded (uninoculated) trees. Traps on infected trees caught 97 percent of all beetles trapped. The size of the bleeding cankers was positively correlated with the response of beetles to infected trees. Both the number of beetles trapped on infected trees prior to any attacks and the intensity of beetle attacks predicted progression to advanced disease stage later in the year. We conclude that beetles naturally adapted to infest recently killed oaks are exploiting a new resource and in the process are accelerating the rate at which *P. ramorum* kills these trees.

Keywords: Phytophthora ramorum, Quercus agrifolia, Quercus kelloggii, Lithocarpus densiflorus, bark and ambrosia beetles.

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[2] Center for Forestry and Integrated Hardwood Rangeland Management Program, University of California, Berkeley 94720. e-mail: aoxomoxo@nature.berkeley.edu; Rick.Standiford@ucop.edu.

[3] Department of Environmental Science Policy and Management, Division of Organisms and Environment, University of California, Berkeley 94720. e-mail: bigwood@nature.berkeley.edu.

[4] United State Department of Agriculture. Forest Service, Pacific Southwest Research Station, Albany, CA 94710. e-mail: smori@fs.fed.gov.

[5] University of California Cooperative Extension, 1682 Novato Blvd., Novato, CA 94947. e-mail: psvihra@comcast.net.

[6] Department of Environmental Science Policy and Management, Division of Ecosystem Science, University of California, Berkeley 94720. e-mail: mkelly@nature.berkeley.edu)

Introduction

The causal agent of sudden oak death was determined to be a *Phytophthora* species by summer 2000 (Rizzo and others 2002). However, this pathogen, *P. ramorum*, was probably present in coastal California forests since the early 1990s. A large proportion of the woody plant species in these forests are hosts (Rizzo and Garbelotto 2003), but because oaks and tanoaks (*Lithocarpus densiflorus*) are more consistently killed than any other species, the epidemic has probably been a significant factor in changes in forest composition for at least 15 years in the most heavily impacted areas. Any comprehensive evaluation of its impact is constrained by the fact that significant damage had already been done by the time this pathogen was found in these forests. As a consequence of this delay in initiating studies of its effects, there is considerable uncertainty in reconstructing subsequent changes in the species composition of these forests, as well as their ecology. This paper presents a summary of our research on the disease known as sudden oak death and attempts to synthesize some results from these various studies.

In March 2000, we established 20 plots in Marin Co. to better understand the nature of this unidentified disease that was killing large numbers of oaks and tanoaks. Our field observations suggested the involvement of a pathogen in the disease syndrome, but in the absence of a confirmed causal agent, speculation included such factors as acid precipitation, air pollution, aerial application of herbicides, and ill-defined “oak decline”.

The principal limitation of these disease progression plots is that the results cannot be reliably extrapolated to watersheds or landscapes, because these plots were not randomly placed, and thus may not be representative of other sites. In order to obtain estimates of disease behavior that might be more broadly applicable, in June (Marin Co.) and October (Santa Cruz Co.) 2001, we initiated landscape-scale studies to evaluate the extent and distribution of the disease in oaks and tanoaks.

Extensive tunneling by ambrosia and bark beetles restricted to *P. ramorum*-induced cankers is common on infected oaks and tanoaks, but is not consistent with previously reported behaviors of these insects (Chamberlain 1958; Furniss and Carolin 1977). In July 2002, we initiated experiments to evaluate the possible roles of bark and ambrosia beetles, by inoculating coast live oaks (*Q. agrifolia*) with *P. ramorum*, applying insecticide to half the trees, and monitoring beetle responses to trees and tree responses to the different treatments.

The studies summarized here focus on interrelated facets of the disease, primarily in coast live oaks. The goal of the disease progression study was to determine the time course of the disease, the involvement of associated secondary organisms, and any characteristics of the host tree that affected the likelihood of infection and its outcome. The goal of the landscape-scale study was to use an unbiased spatial sampling method to map the distribution of the disease and its impact across two different forest types with patchy species distributions, to monitor change over time, and to determine if any quantifiable environmental variables could be used to predict disease incidence and severity.

Methods

Disease Progression.

Twenty disease progression plots were established in Marin Co. in March 2000, ten each in China Camp State Park (CCSP) and in Marin Municipal Water District (MMWD). We monitored every coast live oak, black oak (*Q. kelloggii*), and tanoak larger than five cm dbh (diameter at breast height) in each plot (mean number of trees = 48.3, Standard Error = 2.6) four times per year through 2003, then twice every year thereafter. Symptoms of sudden oak death and associated secondary organisms were recorded, including bleeding, beetle attacks, and reproductive structures of *Hypoxylon thouarsianum*, a fungus that consistently appears in the latter stages of the disease. Data were analyzed for relationships among the primary observable disease symptom of bleeding and the variables beetle attacks and stem dbh. Survival analysis was conducted using a Weibull regression model to identify variables that were associated with increasing probability of tree mortality, for both coast live oaks and tanoaks.

Landscape-scale Studies

In 2001, we placed an array of linear transects in China Camp State Park, where the dominant hosts are coast live oaks and black oaks, and in Soquel Demonstration State Forest (SDSF), where tanoaks and Shreve oaks (*Q. parvula* var. *shrevei*) are the dominant hosts. The *P. ramorum* epidemic has been characterized by a patchy distribution of infected areas within noninfected forest stands (Rizzo and Garbelotto 2003). We established a series of permanent sampling transects to collect detailed measurements of disease incidence in oaks and tanoaks, as well as the associated vegetation. The point-centered-quarter density estimation method (Engemann and others 1994) was chosen to permit us to cover large areas of land, with minimal expenditure of time spent at each sampling location. On each site, we placed parallel transects 0.5 km apart, with sampling nodes every 100 m. The distance, azimuth, dbh, and disease status were recorded for the closest oak or tanoak in each of four cardinal directions at each sampling node, and reevaluated in 2004 (CCSP) and in SDSF during 2003 and 2005. In addition, at each node, we used a 10-factor prism to provide an estimate of the basal area of all woody stems, by species. Transect length varied considerably within each site, with a total of 95 nodes in CCSP and 135 in SDSF.

Beetle Response Study

Two coast live oak-dominated sites in Marin Co. were selected in 2002 to study the effects of beetle attacks on disease progression. A total of 80 coast live oaks were inoculated by removing a bark disk, placing an agar plug of *P. ramorum* directly on the sapwood surface, then replacing the bark. Another 40 trees were wounded but not inoculated, to control for beetle attraction to wounds alone. The synthetic pyrethroid insecticide permethrin was applied to half the trees in each group to control beetle attacks. Beetles were collected periodically in 2003 from sticky traps hung on each insecticide-treated tree and were analyzed by collection date, tree treatment status, size of the canker, and disease stage in December 2003.

Results

Disease progression

In the disease progression study we found that large proportions of the host trees were symptomatic in 2000, with the incidence of infections approximately stable through 2006 in coast live oaks and increasing in black oaks and tanoaks (*table 1*).

Table 1—Percentages of oaks and tanoaks in Marin Co. disease progression plots that were bleeding or dead with bleeding, from 2000 through 2006.

Host Species	2000 Percent Bleed/Dead with bleeding	2003 Percent Bleed/Dead with bleeding	2006 Percent Bleed/Dead with bleeding
Coast live oak	25.0 / 5.8	23.6 / 17.4	25.0 / 22.9
Black oak	15.7 / 3.8	25.0 / 9.4	36.2 /13
Tanoak	39.0 / 8.3	62.4 / 22.2	75.9 / 32.0

The proportion of newly symptomatic coast live oaks has increased at a steady rate in the plots since the initiation of the study (*fig. 1*). A plot of the total disease impact (defined as the percentage of trees that are symptomatic and dead with evidence of bleeding) shows that sudden oak death continues to have severe effects on this species in Marin Co. (*fig. 2*).

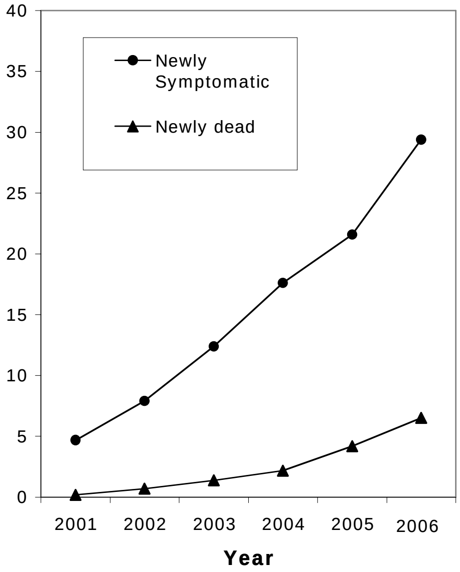

Figure 1—Cumulative percentages of newly symptomatic and dead coast live oaks, determined for each March sampling date, 2001 through 2006.

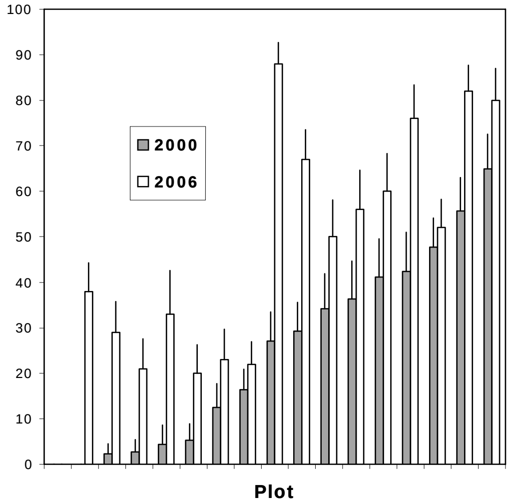

Figure 2—Combined proportion of coast live oaks that were bleeding and dead, by plot, for China Camp State Park, in 2000 (closed bars) and 2006 (open bars).

Beetle attacks have been consistently detected in 40 to 60 percent of bleeding coast live oaks in every year since 2000. The median Weibull survival estimated for bleeding coast live oaks in CCSP that had not been colonized by beetles was 7.0 (1.2) y, decreasing to 2.6 (0.3) y for trees that had been attacked by beetles, with similar results for tanoaks (McPherson and others 2005) For coast live oaks, black oaks, and tanoaks, dbh was positively correlated with the probability of developing infection. Larger diameter infected coast live oaks were more likely to be attacked by beetles. Extensive beetle tunneling was found in 93 percent of the bleeding coast live oaks, both living and dead, that failed on the main stem. This study documented the consistent association of bark and ambrosia beetles with diseased coast live oaks and black oaks and their near-ubiquity in those that eventually died.

Landscape-scale Studies

In both landscape-scale studies, (Marin and Santa Cruz Cos.), we found that the percentage of coast live oaks that were symptomatic declined between 2001 and 2004 (Marin Co.) and 2005 (Santa Cruz Co.) (*tables 2 and 3*). In contrast, the percentage of infected tanoaks and Shreve oaks increased in Santa Cruz Co. Tree death, the ultimate measure of the impact of this pathogen, doubled in coast live oaks from 2001 to 2004 (Marin Co.) and increased sharply for all species by 2005 (Santa Cruz Co.). Through 2004, between 50 and 60 percent of bleeding coast live oaks in Marin Co. were attacked by beetles.

Table 2—*China Camp State Park, point-centered quarter sampling of symptomatic and dead trees, 2001 and 2004. Shown are percentages of living trees (Bleeding) and percentages of all trees (Dead).*

	Percent Bleeding		Percent Dead with Bleeding	
Species	2001	2004	2001	2004
Coast live oak (n = 364)	22	15	6	16
Black oak (n = 52)	24	28	15	25

Table 3—*Soquel Demonstration State Forest, point-centered quarter sampling. Categories are the same as in Table 2.)*

	Percent Bleeding			Percent Dead (all trees)		
Species	2001	2003	2005	2001	2003	2005
Tanoak (n = 406)	14	15	29	2	2	11
Shreve oak (n = 100)	<2	2	22	1	6	17
Coast live oak (n = 26)	15	16	8	0	4	14

In China Camp State Park, the mean annual percentage of coast live oaks that became newly symptomatic was somewhat higher in the disease progression plots, 3.7 percent, than in the plotless landscape-scale evaluation, 1.6 percent. A comparison of infection levels in the two forests suggests that the epidemic began later in SDSF and may still be in the expansion phase.

Beetle Response Study

The inoculation of asymptomatic coast live oaks produced the disease symptoms and variation in their expression observed in naturally infected trees. This was reflected in the variation in canker size among trees, from 0.008 m^2 to 1.13 m^2. Beetles attacked five percent of the inoculated trees within three months of inoculation, prior to the development of bleeding. Although permethrin was applied to half the trees with the expectation that beetle attacks would be prevented, the deterrent effect only lasted about two months after the February 2003 treatment. However, even after beetles breached the insecticide barrier, the mean number of attacks per permethrin-treated tree remained lower than on the untreated trees (Repeated measures ANOVA: $F_{1,53} = 6.4$, $P = 0.014$). Through 2003, the proportion of trees attacked and those that died did not differ between the two treatment groups.

Traps on inoculated trees accounted for 97 percent of all beetles caught in 2003. At each of four sampling dates, beetle counts were greater for inoculated than mock-inoculated trees (Repeated measures ANOVA: $F_{1,52} = 12.56$, $P = 0.001$). Traps on inoculated trees that developed bleeding caught significantly more beetles than those that had never shown bleeding. All the beetle species trapped are classified as saprotrophs and are reported to be restricted to dead trees or dead parts of living oaks. Most of the trapped beetles were in the family Scolytidae, including the ambrosia beetles, *Monarthrum scutellare* (the most abundant species), *M. dentigerum*, *Xyleborus californicus*, *Xyleborinus saxeseni*, and *Gnathotrichus pilosus*, a bark beetle, *Pseudopityophthorus pubipennis*, and *Scobicia declivis* (family Bostrichidae).

The trap catch in April was significantly greater on trees with larger cankers, prior to the first beetle attacks on the permethrin-treated trees (ANOVA: $F_{1,23} = 6.85$, $P = 0.015$). Once beetles attacked the treated trees, subsequent cumulative trap catches were significantly correlated with numbers of entrance holes (repeated measures ANOVA: $F_{1,20} = 29.45$, $P < 0.0001$) but not with canker size.

Canker size in April 2003 was significantly correlated with advanced disease stage (beetle attacks and fruiting structures of *H. thouarsianum*) by December 2003 and in the next two years (ordinal logistic regression, $P < 0.0001$). The trees that died by December 2005 had the largest mean canker size, followed by living trees with beetles plus *Hypoxylon*, and by those that had been attacked by beetles (*fig. 3*).

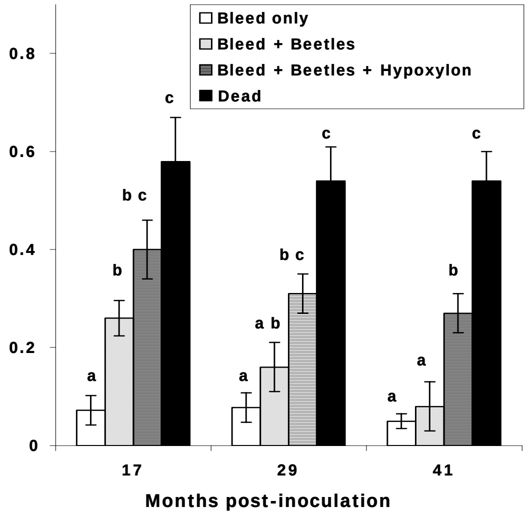

Figure 3—Canker size measured ten months following inoculation predicted the severity of disease stage in inoculated trees at 17 (2003), 29 (2004), and 41 (2005) months post inoculation. Columns for each date labeled with different letters are different ($P < 0.05$).

The numbers of beetles trapped in April, prior to the first beetle attacks on these trees, showed a similar positive relationship with advanced disease stage (*fig. 4*). The trees that attracted the most beetles were those that subsequently were attacked in the greatest numbers and that progressed to advanced disease, and to death.

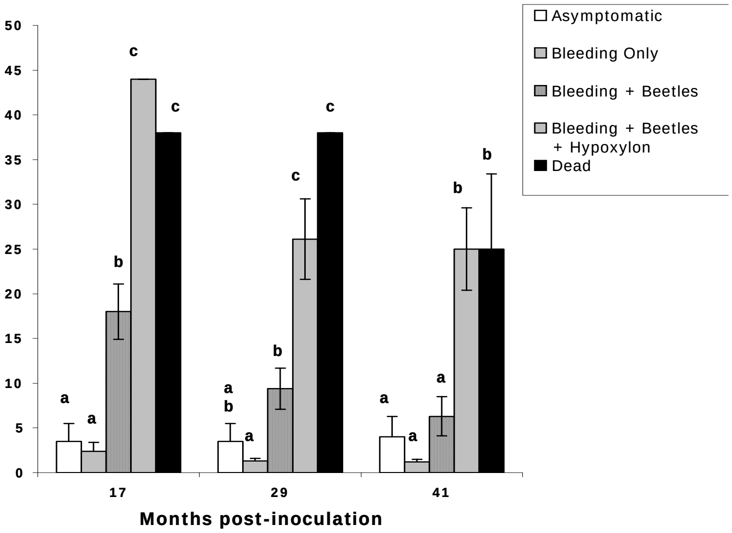

Figure 4—Mean trap catch in April 2003, ten months post inoculation, predicted disease severity, categorized by advanced disease stage. Columns for each date labeled with different letters are different (P < 0.05).

Discussion

The disease known as sudden oak death is now understood to be less sudden and less consistently deadly (Garbelotto and others 2003; McPherson and others 2005) than was initially believed. The consequences for infected forests are nonetheless considerable, having already led to significant losses of oaks and tanoaks, trees whose overall ecological importance in these forests is probably greater than the other host species of *P. ramorum*. Improved understanding of the dynamics of this epidemic will come from studies at different spatial scales that integrate the effects of the insects and fungi that follow the initial infection. It is clear that *P. ramorum* infections in oaks and tanoaks cannot be understood solely as a pathogen-tree interaction and that sudden oak death may be best be described as a disease syndrome involving the pathogen, insects, and fungi.

The rate at which populations of asymptomatic coast live oaks develop infections in the Marin Co. plots does not appear to have declined since 2000. This result was unexpected, as observations of forest canopies for several years after 2001 showed fewer recently killed trees and the percentage of infected living trees has remained relatively stable (*table 1*). However, the approximately constant rate of new infections (*fig. 1*) suggests that although large numbers of the least resistant trees may have been infected early in the epidemic, many of the remaining trees are also susceptible to infection.

The inoculated trees exhibited considerable variation in bleeding canker size, a phenomenon that has been interpreted as reflecting resistance to *P. ramorum* (Rizzo and others 2002; Dodd and others 2005). Resistance may be a transient property of the host. If climatic variation or the activities of such biotic factors as insects and fungi shift the balance toward the pathogen in different years, the disease may progress more rapidly even in trees with smaller cankers. The 3.7 percent average annual rate at which coast live oaks in the Marin Co. study have become newly infected since 2001 forecasts very heavy losses of these trees in years to come. We have shown that *P. ramorum* is more likely to infect larger trees and that, once infected, larger trees are more likely to be attacked by beetles. Since beetle attacks are shown to significantly reduce the median survival of these trees, the production of acorns will be significantly reduced as the epidemic removes larger trees from the forests. The presence of very few seedling or sapling coast live oaks or black oaks in these forests (unpublished observation) indicates that little recruitment was occurring prior to the epidemic. Although seedlings and saplings of the true oaks do not appear to be readily infected (Rizzo and others 2002), there may be few mature specimens remaining after another 25 years with *P. ramorum* as a component of the forest biota. Shifts in species dominance will likely lead to cascading ecological consequences wherever *P. ramorum* has become established in forests with a large component of these or other susceptible oak species.

One factor that emerges from these studies is the consistent role of bark and ambrosia beetles in the weakening and death of infected oaks. Although these beetles are understood to be saprotrophic, restricted to moribund or recently killed oaks, their attacks on *P. ramorum* cankers occur within one to two years following infection, when the foliage appears vigorous and the trees exhibit no visible indications of the general decline expected for trees that are suitable ambrosia beetle hosts. While *P. ramorum* alone causes damaging cankers that may severely compromise tree health by interfering with phloem and xylem transport (Parke and others 2006), beetles that penetrate deep into sapwood may irreversibly disable the defenses of the trees.

These responses of beetles to *P. ramorum*-infected trees may be mediated by volatile compounds released by cankers. The size of the canker may affect the quantity of attractant volatiles released, as well as the surface area suitable for beetle tunneling. Once beetles have tunneled into a tree, their pheromone production likely becomes the dominant attractant for other beetles (Wood 1982; Paine and others 1997). Greater numbers of beetles in a tree will likely lead to increased damage to both phloem and sapwood, as well as the introduction of various decay fungi deep into the sapwood (Svihra and Kelly 2004). Since beetles had attacked approximately half of the coast live oaks in both naturally infected and artificially inoculated stands during any observation period, these insects must be seen as components of the disease syndrome. Once beetles initiate attacks on an infected tree, their pheromone production probably leads to an irreversible decline in the health of the tree as beetle attacks increase.

The landscape-scale and plot studies are demonstrating that sudden oak death continues to change the ecological roles of susceptible oak species and tanoaks in coastal California forests. The beetles that follow the infection are secondary in temporal sequence, but may significantly inhibit the ability of infected trees to defend against the pathogen. Studies presently under way in our lab should better define the sequence of beetle and fungal activity in infected coast live oaks and help to clarify their roles in tree death.

Acknowledgements

We wish to acknowledge the assistance of numerous field and laboratory workers, especially Dan Stark, Andrew Nelson, Nicole Palkovsky, Kim Kiernan, Janice Alexander, and Gabriela Ritok-Owens. David Rizzo provided *Phytophthora ramorum* cultures. Land managers in China Camp State Park, Marin Municipal Water District, Marin County Open Space District, and Soquel Demonstration State Forest have been supportive of this research. Funding has been provided by the University of California Division of Agriculture and Natural Resources, The University of California Exotic/Invasive Pests and Diseases Research Program, the California Department of Forestry, and the US Forest Service Pacific Southwest Research Station.

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Continue

Impacts of *Phytophthora ramorum* Canker and Other Agents in Sonoma County Forests[1]

Tedmund J. Swiecki[2] and Elizabeth A. Bernhardt[2]

Abstract

To study impacts of sudden oak death (SOD), a lethal bark canker disease caused by *Phytophthora ramorum*, we established permanent plots in Sonoma County forest types at risk of SOD. Baseline stand and tree health data were collected in 2001 and the plots were reassessed in 2004. The 250 plots (0.02 ha each) were located at 11 study locations in stands containing *Quercus agrifolia*, *Q. kelloggii*, or *Lithocarpus densiflorus* as the dominant hardwood species. By 2004, *P. ramorum* canker symptoms developed at two locations that lacked symptoms in 2001, leading to new tree mortality at one of these locations. Between 2001 and 2004, plot level incidence of *P. ramorum* canker increased from 29 to 40 percent of plots containing *L. densiflorus* and from 2 to 10 percent in plots containing *Q. kelloggii*. Plots with *Q. agrifolia* showed a slight drop in *P. ramorum* canker (from 9 to 7 percent of plots) due to apparent symptom remission in trees at one location. Between 2001 and 2004, the percentage of trees with *P. ramorum* canker symptoms increased at three of four locations with symptomatic SOD canker hosts. Mortality due to both *P. ramorum* and other agents increased at 9 of 11 study locations between 2001 and 2004. Among SOD canker hosts that died during this period, mortality was due to *P. ramorum* in 4 of 16 *Q. kelloggii*, 7 of 18 *Q. agrifolia*, and 18 of 50 *L. densiflorus*. In most study locations, annual background mortality unrelated to *P. ramorum* was less than 1 percent per year between 2001 and 2004. Over this same period, mortality due to *P. ramorum* exceeded background mortality at three locations and equaled it at a fourth. At one *L. densiflorus* location, mortality associated with an unidentified bark canker was comparable to levels of mortality associated with *P. ramorum* at other locations. Only *P. nemorosa* and *P. pseudosyringae* were isolated at this location.

Keywords: California black oak, coast live oak, Lithocarpus*, mortality,* Quercus*, SOD, sudden oak death, tanoak.*

Introduction

Phytophthora ramorum has become established in native forests in a number of counties in Northern and Central California, including Sonoma County. Host trees that can be killed by *P. ramorum* canker (sudden oak death or SOD), including tanoak (*Lithocarpus densiflorus*), coast live oak (*Quercus agrifolia*), and California black oak (*Q. kelloggii*), are important components of many Sonoma County forests and woodlands. Elevated mortality of these SOD canker hosts due to *P. ramorum* canker has the potential to severely impact many important forest ecosystems in Sonoma and other counties.

In summer 2001, with funding provided by the Sonoma County Fish and Wildlife Advisory Board, we established a set of permanent research/monitoring

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[1] Abbreviated version of this paper was presented at the Sixth California Oak Symposium: Today's Challenges, Tomorrow's Opportunities, October 9-12, 2006, Rohnert Park, California.

[2] Principal and Plant Pathologists, Phytosphere Research, 1027 Davis Street, Vacaville, CA 95687.

plots in Sonoma County woodlands and forests at risk due to *P. ramorum* canker (Swiecki and Bernhardt 2001). Primary objectives of this initial project were to assess overall disease impacts in various forest types and establish baseline conditions against which future changes could be measured. Targeted stands were those with a major component of tanoak, coast live oak, and/or California black oak.

Once baseline conditions within plots had been established, subsequent assessments of the plots were to be used to document the rate and pattern of disease spread within stands and disease progress in individual trees. As part of a project funded by the USDA-Forest Service, the plots established in 2001 were reevaluated in the summer of 2004 (Swiecki and Bernhardt 2005). The objectives of this second project were to estimate the overall impact of SOD on affected forest types and to monitor the spread of disease over time. In this paper, we report on changes in disease distribution, tree mortality, and overall tree health in these plots between summer 2001 and summer 2004.

Methods

In the summer of 2001, we established 250 plots at eleven locations throughout Sonoma County where tanoak, coast live oak, and/or California black oak were common (*table 1*). Plots were circular with a radius of 8 m measured parallel to the ground slope (plot area 0.02 ha=0.05 acre). Plots at each location were established at vertices of a grid superimposed over a map of the location and are unbiased with respect to tree condition or the presence or absence of disease. The only requirements for establishing a plot at a grid intersection was that SOD canker host species (coast live oak, California black oak, and/or tanoak) were present and the slope was navigable (generally no greater than about 70 percent slope). The nominal spacing between grid points was 50 m as plotted on a topographic map, with the exception of the first location (Jack London SP), where the grid spacing was 60 m. Ground distances between plot centers are generally greater than 50 m because of ground slope. Because only plots containing SOD canker host were sampled, the pattern of sampled plots often differs from the idealized sampling grid. The overall area represented by the sampled plots in each grid varied from about 4.7 to 14 ha (*table 1*), depending on the distribution of the host trees at each location. The sampling plan is described in detail in Swiecki and Bernhardt (2001).

We used a handheld GPS receiver (Garmin® GPS 76) with a high-gain external Gilsson® GPS antenna mounted on a telescoping mast to geolocate the specified plot vertices during plot establishment in 2001 and to relocate plots in 2004. One to several trees in or near each plot were marked with numbered aluminum tree tags in 2001. We also recorded the distance and azimuth from tagged trees to each plot center to permit precise relocation of plot centers.

Table 1—*Study locations and numbers of plots, approximate areas, and host species present at each.*

Location	Abbreviation	Number of plots	Approximate plot grid area[1] (ha)	SOD canker host species
Jack London State Park	JLSP	24	8.2	Cal. black oak, tanoak, coast live oak
Sugarloaf Ridge State Park	SRSP	25	6.7	coast live oak
Lake Sonoma (Army Corps of Engineers)	LS	24	8.8	coast live oak, Cal. black oak
Weston (private land)	Weston	26	7.2	coast live oak, Cal. black oak
Austin Creek State Recreation Area	ACSRA	25	7.5	tanoak, Cal. black oak
Modini (private land)	Modini	25	14.0	Cal. black oak, coast live oak
Annadel State Park	ASP	24	7.5	Cal. black oak
Salt Point State Park	SPSP	18	5.5	tanoak
Helen Putnam Regional Park	HPRP	24	5.3	coast live oak, Cal. black oak
Foothill Regional Park	FRP	15	4.7	Cal. black oak, coast live oak
Sonoma Coast State Beach	SCSB	21	6.4	tanoak

[1] Plot grid areas were estimated by drawing an irregular polygon around the plots at each location using ArcView® GIS software. Polygon edges were set approximately 30 m beyond plot centers.

Trees were included in plots if the edge of the main stem was within 8 m of the plot center. A hand-held laser rangefinder (Leica® Disto Classic) was used to determine which trees were within a plot. In each plot, we collected detailed disease data on up to three tagged SOD canker host trees in or near each plot. These trees are referred to as tally trees. Tally trees were sometimes located beyond the 8 m plot boundary in plots that had few live SOD canker host trees. These out-of-plot tally trees are considered only in calculations related to change in disease status and disease on a percentage basis, but are excluded from plot-based density calculations.

All other SOD canker host trees in the plots were categorized with respect to species, canopy position (overstory or understory) and disease status. We noted the type and extent of *P. ramorum* canker symptoms present and whether the tree was in decline or dead due to other agents. We also noted changes in the status of trees other than canker hosts in the plots (for example, decline or mortality). Other plot data evaluated included overall tree cover, California bay (*Umbellularia californica*) cover, the presence of *P. ramorum*-like foliar symptoms on California bay, poison oak (*Toxicodendron diversilobum*) cover, shrub species present, overall shrub cover, canker host regeneration, and the presence of other disease agents in the plot.

In 2001, some suspected *P. ramorum* cankers were sampled for pathogen isolation by Steven Swain (then with Sonoma County UC Cooperative Extension). Most of those isolations were conducted in the late summer of 2001. In the 2004 resurvey, we conducted additional sampling for pathogen isolation, primarily to (1) determine whether *P. ramorum* was present at locations where it had not been found previously, (2) clarify the infection status of trees in known *P. ramorum*-infested areas that had ambiguous or atypical symptoms, or (3) determine whether other *Phytophthora* spp., including *P. nemorosa* and/or *P. pseudosyringae*, were present at locations with symptomatic trees. In particular, numerous symptomatic plants were sampled at Austin Creek in 2004 to determine whether any of the cankers at this site were caused by species other than *P. ramorum*.

Most isolations were made from stem cankers on SOD canker hosts or from California bay leaves, but a few other host species were also sampled (*table 2*). Tissue pieces from sampled plants were placed into PARP agar plates (Erwin and Ribeiro 1996) to confirm the presence of *P. ramorum* or other *Phytophthora* species. Plates were transported to the lab of Dr. David Rizzo at UC Davis for incubation and identification of fungi that grew out on the PARP plates.

Data Management and Analysis

Data summaries and analyses were prepared using JMP® statistical software, version 5.1.2 (SAS Inc., Cary NC). We used the likelihood ratio chi square test to test for independence of variables in two-by-two or larger contingency tables. We used paired t-tests to test for mean differences in continuous variables recorded for individual plots in 2001 and 2004. Unless otherwise indicated, effects or differences are referred to as significant if $p \leq 0.05$.

Results

The densities of SOD canker hosts at each study location are shown in *figure 1*. A total of 460 coast live oak, 373 California black oak, and 645 tanoak trees were included in the study. Tally trees, for which the most detailed health data was collected, included 229 coast live oaks, 251 California black oaks, and 180 tanoaks. As shown in *figure 1*, California bay, an epidemiologically important foliar host of *P. ramorum*, was present within plots at 7 of the 11 study locations.

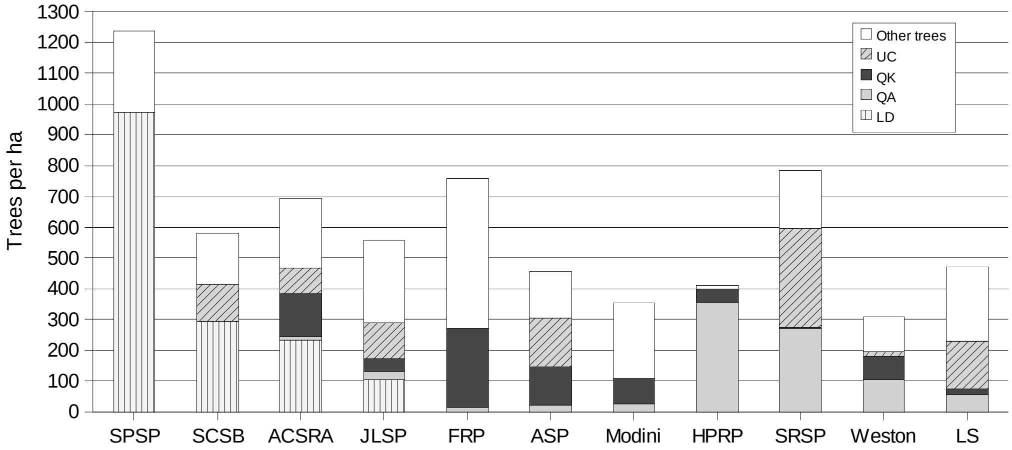

Figure 1—Composition of forests at each study location in trees/hectare. LD=*Lithocarpus densiflorus*; QA=*Q. agrifolia*; QK=*Q. kelloggii*; UC=*Umbellularia californica*; Other trees=other oak, hardwood, and/or conifer species.

Presence of P. ramorum *and Other* Phytophthora *Species at Study Locations*

At the time of the original 2001 survey, sampling conducted by members of David Rizzo's lab at the University of California, Davis, had confirmed the presence of *P. ramorum* at three of the study locations: Jack London, Sugarloaf Ridge, and Austin Creek. No additional locations had positive confirmations of *P. ramorum* as the result of sampling of suspected *P. ramorum* cankers in 2001.

The results of the more extensive sampling conducted in 2004 are shown in *table 2*. In 2004, *P. ramorum* was the only *Phytophthora* species isolated from stem cankers or California bay foliage at the three locations (Austin Creek, Jack London, and Sugarloaf Ridge) that were known to have *P. ramorum* in 2001.

Two locations, Annadel and Lake Sonoma, lacked *P. ramorum* symptoms in 2001 but were confirmed as having *P. ramorum* present in 2004. At Annadel, several California black oak trees showed canker symptoms in 2004 typical of those caused by *P. ramorum,* and isolations confirmed its presence in trees in three plots. *P. ramorum* was also isolated from cankers on a coast live oak near a fourth plot. In addition, many California bay trees showed typical symptoms of leaf infection by *P. ramorum*, and *P. ramorum* was confirmed on California bay leaves from eight plots.

We recovered *P. ramorum* in 2004 from symptomatic California bay foliage from trees located along a small stream between plots at Lake Sonoma. Foliar symptoms in California bay were only observed in this portion of the Lake Sonoma plot grid, and no symptomatic oaks were observed in 2004. We had noted two California black oaks trees with atypical bleeding bark cankers near this area in 2001, but these cankers had become inactive by 2004 and did not appear to be typical of active or inactive *P. ramorum* cankers. Tissue sampled from one of these two trees in 2004 did not yield any *Phytophthora* spp.

Table 2—*Number of positive* Phytophthora *isolations out of the total number of units sampled in 2004 at various study locations. Sampling units were individual trees for stem cankers and single trees or localized groups of trees or plants for the foliar symptoms.* P. ramorum *was the only* Phytophthora *species present in positive isolations with the exception of the Sonoma Coast samples, which yielded both* P. pseudosyringae *and* P. nemorosa.

Location	California bay	Tanoak	California black oak	Coast live oak	Coast redwood	Douglas-fir
Salt Point		0/14[1]				
Sonoma Coast	3/4[2]	0/7				
Austin Creek	13/16	14/16	1/2		2/2	0/1
Jack London	1/1		0/1			
Annadel	8/9		3/3	1/1		
Helen Putnam				0/4		
Sugarloaf Ridge	2/2			1/4		
Weston	0/4			0/2		
Lake Sonoma	1/2		0/1			

[1] An additional isolation from California huckleberry (*Vaccinium ovatum*) was also negative.

[2] Leaves from one tree yielded *P. pseudosyringae*; leaves from two other trees yielded *P. nemorosa*.

Sonoma Coast was the third location where *Phytophthora* spp. was newly isolated in 2004. *P. nemorosa* and *P. pseudosyringae* were isolated from leaves of California bay, which is common at this location (*fig. 1*). However, *P. ramorum* was not isolated from California bay leaves or tanoak cankers sampled at this location (*table 2*).

Bark cankers were present on about 20 percent of the tanoaks at Sonoma Coast *(fig. 2*), but canker symptoms on tanoaks at this location were generally not typical of those caused by *P. ramorum*. Many of the cankers that had recent bleeding in 2004 were small and did not appear to be very aggressive. Many cankers originally noted in 2001 appeared inactive in 2004, with no recent bleeding, and some had callus development at the old canker margin. In some trees, the bark was only affected to a shallow depth. The phloem tissues in these shallow cankers subsequently decayed to a light-colored, powdery consistency and eventually sloughed off, leaving a somewhat eroded appearance to the bark surface.

No other likely causes of the bark cankers at Sonoma Coast were identified. Other pathogens observed on tanoak at this location included *Cryphonectria gyrosa*, which causes stem cankers but is readily recognized by its distinctive sporulation, and the root pathogens *Armillaria* spp. and *Inonotus dryadeus*.

A small number of tanoaks at Salt Point had bark cankers similar to those seen at Sonoma Coast *(fig. 2*). These included the non-aggressive shallow cankers that decayed to form a light powdery material. We also observed numerous callused cankers with exposed wood in the center, similar to canker rot cankers seen in some oaks. None of the tanoak cankers sampled at this location yielded any *Phytophthora* spp. No California bay trees are present within the plot grid for sampling.

Especially at Sonoma Coast, many trees with extensive cankers were subsequently attacked by ambrosia beetles (*Monarthrum* spp.) and the sapwood-decaying fungus *Hypoxylon thouarsianum* (*fig. 2*). Tree mortality associated with these stem cankers increased substantially at both Salt Point and Sonoma Coast between 2001 and 2004.

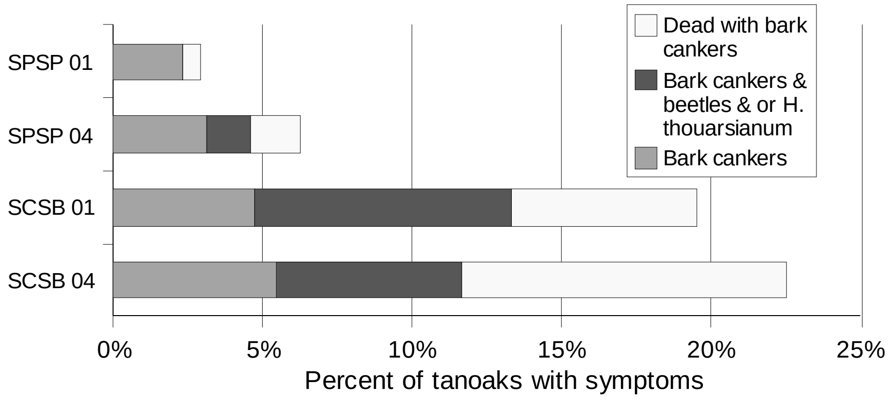

Figure 2—Incidence of symptoms in tanoak associated with an unidentified bark canker at Salt Point (SPSP) and Sonoma Coast (SCSB) in 2001 and 2004. Symptom classes are analogous to the early, late, and dead classification system used for *P. ramorum* canker *(fig. 3*).

Changes in P. ramorum *Disease Levels*

The proportion of trees with *P. ramorum* canker symptoms increased at the two tanoak locations with known *P. ramorum* infestations, and in the new disease front at Annadel (*fig. 3*). The increase in the proportion of symptomatic trees was most dramatic at Austin Creek, nearly tripling since 2001. However, the proportion of symptomatic trees at Sugarloaf Ridge actually declined slightly between 2001 and 2004 due to the apparent remission of canker symptoms in some trees. All four locations showed an increase in the proportion of trees killed by *P. ramorum* (*fig. 3*).

Across the four locations shown in *figure 3*, the percentage of plots that had trees with *P. ramorum* canker symptoms increased from 22 to 38 percent. The percent of plots with *P. ramorum* canker symptoms on California black oak and tanoak increased, but the percentage of plots with *P. ramorum* canker symptoms on coast live oak decreased slightly between 2001 and 2004 (*table 3*). The slight drop in the incidence of *P. ramorum* canker symptoms in coast live oak was due to apparent symptom remission in two trees at Sugarloaf Ridge, which were the only symptomatic trees in their respective plots.

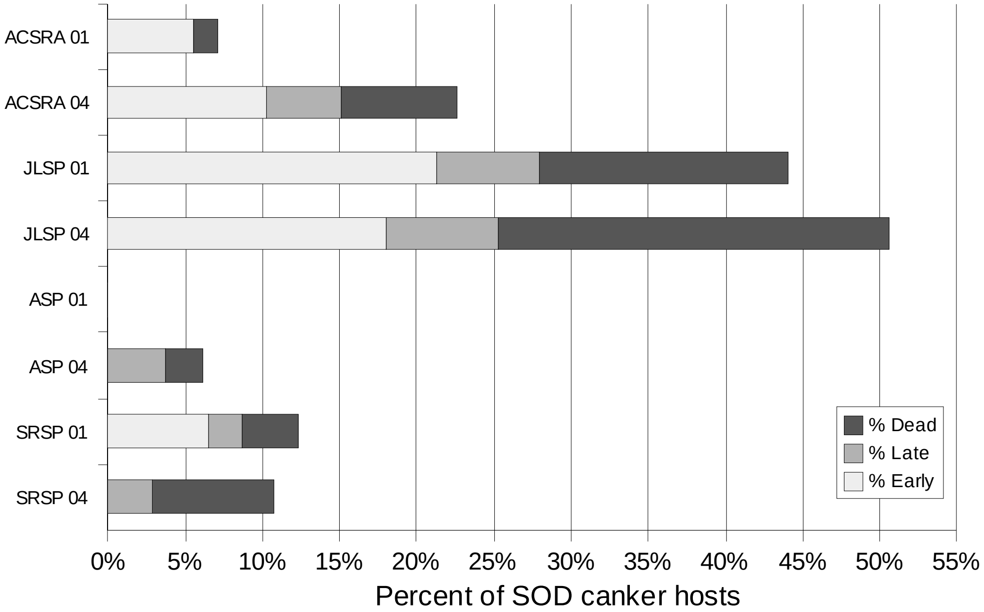

Figure 3—Changes in *P. ramorum* symptom classes between 2001 and 2004 at Austin Creek (ACSRA), Jack London (JLSP), Annadel (ASP), and Sugarloaf Ridge (SRSP). Early = bleeding cankers only; Late = cankers and associated sporulation of *Hypoxylon thouarsianum* and/or damage by wood boring beetles, primarily ambrosia beetles (*Monarthrum* spp.); Dead = entire tree killed by *P. ramorum* canker. Multistemmed trees with both live stems and stem(s) killed by *P. ramorum* were classified as having late disease symptoms.

Table 3—*Percent of plots with SOD symptoms on canker host species in 2001 and 2004.*

Year	California black oak (119 plots)	coast live oak (114 plots)	tanoak (73 plots)
2001	2	9	27
2004	10	7	40

In comparing the spatial distribution of disease in 2001 and 2004, it appeared that disease distribution was relatively static at Jack London and Sugarloaf, and was spreading from one or more disease loci within the plot grids at Annadel and Austin Creek. At all four locations, symptoms on California bay were more widely distributed than were *P. ramorum* cankers on the canker host species. Furthermore, plots with *P. ramorum* canker were commonly adjacent within the plot grid to other plots with symptomatic trees, especially in the 2004 evaluation. This pattern was especially evident at Austin Creek. Between 2001 and 2004, disease appeared to expand outward from areas that had infected trees in 2001 *(fig. 4*).

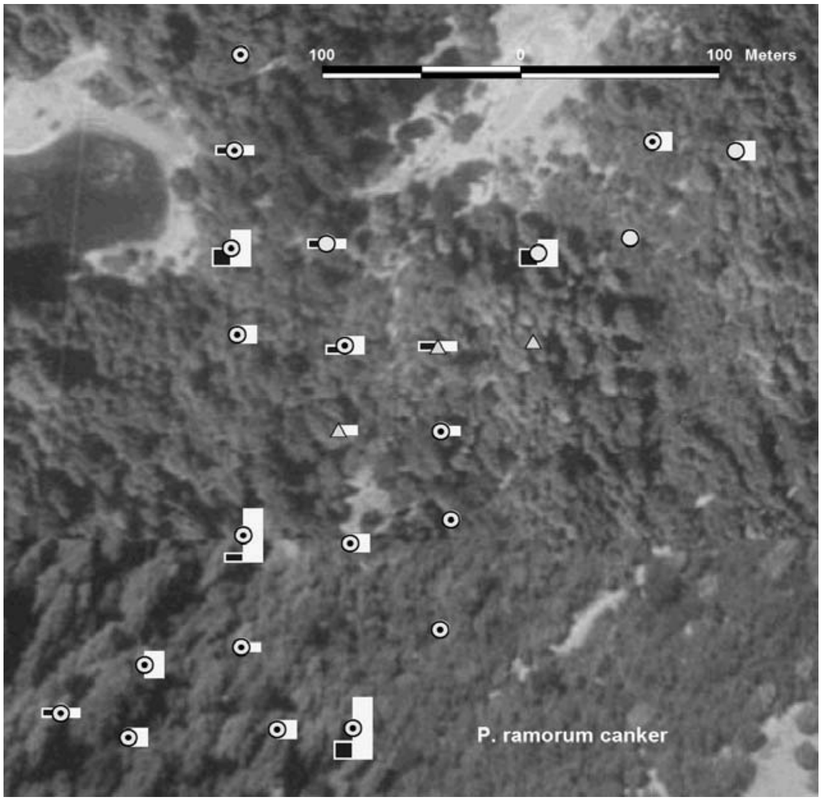

Figure 4—Distribution of *P. ramorum* symptoms in Austin Creek plots in 2001 (dark bar to left of symbol) and 2004 (light bar to right of symbol). Bars indicate the number of symptomatic SOD canker hosts, including trees in plots and additional tagged trees beyond plot edges. The minimum bar height shown indicates one tree. Symbols indicate plot locations. Plots containing California bay are denoted with circles; a black dot in the center of the circle indicates that *P. ramorum* symptoms were present on California bay foliage. Plots without California bay are denoted with triangles.

Mortality of SOD Canker Host Trees

Between 2001 and 2004, mortality increased among all SOD canker hosts *(fig. 5*) and the percentage of plots with mortality also increased (*table 4*). Between the 2001 and 2004 evaluations, the number of dead California black oak trees more than doubled, from 13 to 29, whereas coast live oak and tanoak showed smaller relative increases in mortality. *P. ramorum* contributed to the increase in mortality between 2001 and 2004 in each species, accounting for 4 of 16 dead California black oaks, 7 of 18 dead coast live oaks, and 18 of 50 dead tanoaks. Among all mortality rated in 2004 (that is, all trees estimated to have died after 1991), *P. ramorum* was responsible for 5 of 29 dead California black oaks, 12 of 41 dead coast live oaks, and 31 of 116 dead tanoaks.

Mortality due to agents other than *Phytophthora* spp. was mostly due to wood decay fungi. Important pathogens we observed on oaks and/or tanoaks in plots included *Inonotus andersonii*, *I. dryophilus*, *I. dryadeus*, *Ganoderma* spp., *Laetiporus gilbertsonii*, and *Armillaria* spp.

Table 4—*Percent of plots with dead trees of SOD canker host species in 2001 and 2004.*

Year	California black oak (114 plots)	coast live oak (119 plots)	tanoak (73 plots)
2001	10	18	49
2004	20	25	67

Levels of mortality due to both *P. ramorum* and other agents varied between study locations. Tree mortality due to *P. ramorum* canker greatly exceeded mortality due to other causes at both Austin Creek and Jack London *(fig. 5*). At Sugarloaf Ridge, mortality due to *P. ramorum* canker approached, but was less than, mortality due to other agents. At Annadel, where *P. ramorum* canker symptoms first appeared in the 2004 evaluation, mortality due to other causes was still much more prevalent than mortality due to *P. ramorum*.

The overall mortality percentages shown in *figure 5* include trees rated in the 2001 survey as having died within the previous 10 years. Hence, the data for 2004 bars in these figures represent 13-year estimated mortality. In contrast, mortality occurring between the 2001 and 2004 evaluations does not include uncertainties associated with the year of mortality of trees that were dead in 2001. We used both 2001to 2004 observed mortality and the 1991 to 2001 estimated mortality rates to calculate annual mortality rates for all locations *(fig. 6*).

Estimated annual background mortality rates for the 2001 to 2004 interval were close to or somewhat higher than those for the 1991 to 2001 interval for most locations. Two locations, Foothill and Helen Putnam, had no new mortality among SOD canker hosts between 2001 and 2004. Overall, the background mortality rate was about 1 percent or less per year for both time intervals at all locations. The differences in background mortality rates between and within locations shown in *figure 6* were not significant. In all locations, some tree mortality was associated with wood decay fungi, especially canker rot fungi such as *I. andersonii* and *I. dryophilu*s, and root disease fungi such as *Ganoderma*. This background mortality excludes mortality due to *P. ramorum* canker and the unknown bark canker at Sonoma Coast and Salt Point.

Annual *P. ramorum* mortality rates were higher for 2001 to 2004 than for 1991to 2001 at all four locations with *P. ramorum* canker *(fig. 6*). For these four locations, the annual mortality due to *P. ramorum* canker for the period 2001 to 2004 (2.03 percent per year) was significantly greater than for 1991 to 2001 (0.42 percent per year; likelihood ratio p=0.02). Furthermore, annual 2001 to 2004 mortality due to *P. ramorum* exceeded background mortality during this period at Jack London, Austin Creek, and Sugarloaf Ridge, and equaled it at Annadel *(fig. 6*).

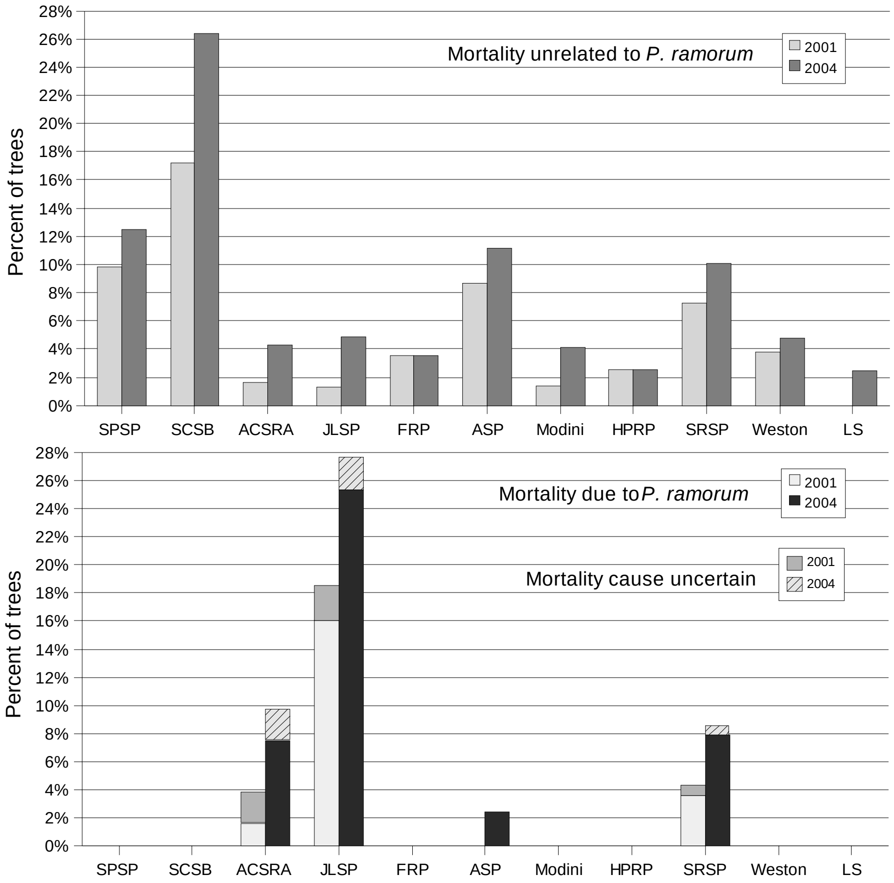

Figure 5—Cumulative mortality among SOD canker host trees due to *P. ramorum* (bottom) and other causes (top) in 2001 and 2004 by location. Mortality in the 2001 survey includes trees rated as having died within the previous 10 years, i.e., mortality since 1991. Total mortality in 2004 covers the period 1991 to 2004. Location abbreviations are shown in *table 1*.

As shown in *figure 6*, recent (2001 to 2004) rates of mortality ascribed to the unidentified bark canker at Sonoma Coast are similar to those due to *P. ramorum* at Austin Creek. Sonoma Coast also had high levels of mortality in 2001 to 2004 that could not be definitively assigned to a given cause (unknown bar in *figure 6*). If some or most of this mortality is also related to the unidentified canker disease, it would further increase the relative importance of this mortality category.

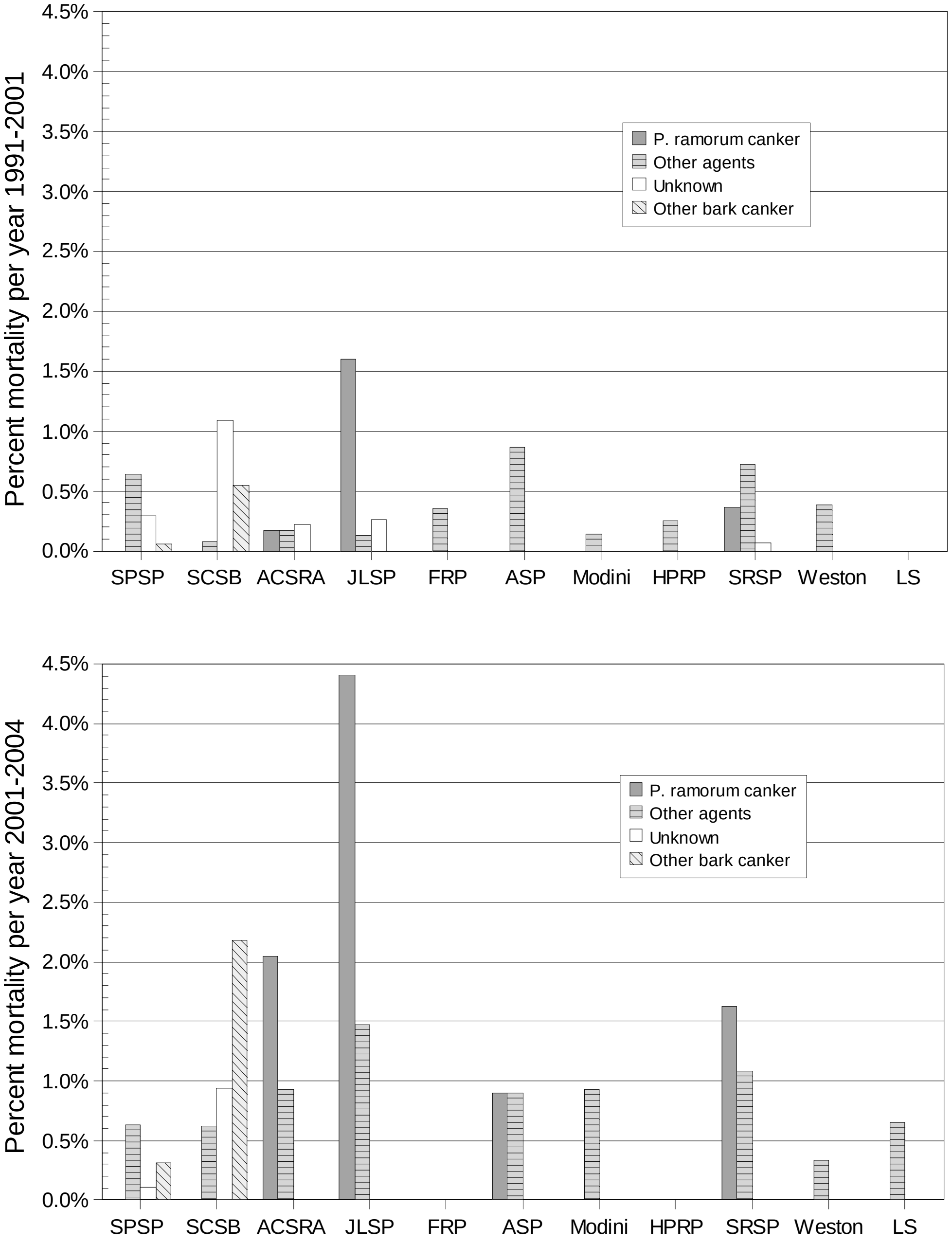

Figure 6—Annual mortality (percent mortality per year) of SOD canker host trees by cause and study location for the periods 1991 to 2001 (top) and 2001 to 2004 (bottom). Location abbreviations are shown in *table 1*.

Discussion

Between 2001 and 2004, *P. ramorum* first appeared within our study areas at two locations: Annadel and Lake Sonoma. Although *P. ramorum* was first confirmed at Annadel SP on bay leaves in July 2003 (Allison Wickland, personal communication; http://kellylab.berkeley.edu/OakMapper/viewer.htm), our isolations were the first reports of *P. ramorum* on SOD canker hosts at this location. Based on the first known appearance of symptoms in canker hosts, it appears that *P. ramorum* had been introduced into Annadel at a later point than it had been at Jack London and Sugarloaf Ridge, two nearby state parks.

Based on its limited distribution, we believe that the observed infestation at Lake Sonoma is also of relatively recent origin. The infested area is located along a creek at the point where it is crossed by a constructed trail that is used by hikers, equestrians, and bicyclists. An unpaved parking lot used primarily for horse trailer parking and equestrian events is located adjacent to the creek upstream from the point where the infestation was detected. It is likely that *P. ramorum* became established in the creek area from infested materials (such as soil or foliage) that were transported to the area by humans and introduced into the creek either via the trail or the parking lot.

These findings suggest that even within counties or regions in which *P. ramorum* is present, preventing transport of the pathogen material into apparently non-infested areas may be an important method for reducing disease impacts. Current regulatory programs at the state and federal level are directed at the prevention of spread from infested counties to other counties or states. Within infested regions, local programs to minimize or prevent intra-county and intra-regional pathogen spread may be needed.

Increases in tree mortality were observed in all locations where *P. ramorum* was found. Given the low rate of new infections at Sugarloaf Ridge and Jack London, it is likely that annual *P. ramorum* mortality rates will decrease at these locations over the next few years. In contrast, due to new infections at Austin Creek and Annadel, annual *P. ramorum*-related mortality rates are likely to stay constant or increase over the next few years.

Different stages of disease spread and progress were seen among the locations with *P. ramorum* infestations. As of the 2004 assessment, Lake Sonoma appeared to represent a site of very recent pathogen introduction; the pathogen had not yet become widely established on California bay and canker hosts were not yet affected. At Annadel, *P. ramorum* was more widely established in 2004, but the disease epidemic in the plot area appeared to be at an early stage. *P. ramorum* had begun to affect some canker hosts as well as California bay, but the epidemic was probably still limited by inoculum production and distribution. At Austin Creek, the pathogen was established in various parts of the plot grid by 2001, and disease progress among the SOD canker hosts appeared to be at an exponential phase between 2001 and 2004. Jack London represents a later phase of the epidemic, in which the pathogen had become well established throughout the plot grid. At this site, many of the trees with the highest disease risk had already been infected by 2001, so the rate of new infections was relatively low between 2001 and 2004.

These results suggest that disease progress among the SOD canker hosts in a newly infested stand may follow a sigmoidal disease progress curve. The percentage of newly-diseased trees probably increases slowly after the initial introduction of the pathogen due to limited inoculum density. As the foliar disease epidemic spreads throughout a stand, disease incidence in canker hosts can increase rapidly under favorable conditions. As the number of uninfected susceptible hosts decreases, the epidemic becomes limited by the lack of suitable hosts. The disease situation at Sugarloaf Ridge may either represent this latter stage of the epidemic or a stalling of the epidemic in the early phase due to environmental conditions that were relatively unfavorable for disease development.

Inoculum production by *P. ramorum* is favored by late spring rainfall, although levels and temporal patterns of inoculum production differ somewhat between mesic tanoak stands and more xeric oak stands (Dave Rizzo, personal communication). Based on our review of weather station data (Western Regional Climate Center 2006), most portions of Sonoma County had average to below average rainfall without high amounts of late spring rain between our 2001 and 2004 evaluations. Disease spread under these conditions may have been relatively low compared with what would be expected under more favorable conditions, such as those that occurred in spring 2005 and 2006. Informal observations indicate that disease levels have increased dramatically in portions of Sonoma County since 2004. Reassessment of these plots in 2007 would allow us to compare disease progress during periods with different levels of inoculum production.

P. ramorum, *P. nemorosa*, and *P. pseudosyringae* were only confirmed at locations that also had substantial amounts of California bay within the plots *(fig. 1*). Previous research has shown a strong epidemiological link between California bay proximity and coast live oak infection rates by *P. ramorum* (Swiecki and Bernhardt 2002). The presence of other foliar hosts, with the possible exception of poison oak (Swiecki and Bernhardt 2003), has not been correlated with infection of California black oak or coast live oak. Futhermore, *P. ramorum* does not normally sporulate on infected bark cankers of its oak hosts (Davidson and others 2005). Hence, California black oaks and coast live oaks at the Helen Putnam, Modini, and Foothill study locations and much of the Weston location may be very unlikely to develop *P. ramorum* canker under current stand conditions. Disease risk at sites containing tanoak is not completely related to California bay presence since tanoak sustains foliar and twig infections that can produce *P. ramorum* inoculum (Rizzo and others 2002). Therefore, tanoak stands in Sonoma County are likely to be at risk from *P. ramorum* for the foreseeable future.

The cause of the bark canker symptoms seen at Sonoma Coast and Salt Point remains uncertain. *P. nemorosa* and *P. pseudosyringae* were isolated from bay leaves in the plots at Sonoma Coast, but we were unable to recover any *Phytophthora* spp. from active bleeding cankers at either location. However, given the relatively low numbers of isolations performed, we cannot rule out *P. nemorosa* and/or *P. pseudosyringae* as possible causes of the cankers. *P. ramorum* also cannot be entirely ruled out as a possibility at this point. However, the fact that *P. ramorum* was not recovered from symptomatic trees in either 2001 or 2004 strongly suggests that this species was either not present or was not associated with the sampled cankers.

P. nemorosa and *P. pseudosyringae* are recently-described species (Hansen and others 2003, Jung and others 2003) and further analysis is needed to determine how long these species have been present in California forests. If most of the cankers at Sonoma Coast are actually caused by one or both of these species, it would imply that these agents may have impacts comparable to *P. ramorum* in at least some locations. The greater importance of this canker disease at Sonoma Coast relative to Salt Point may be related to the fact that California bay, which is also a host of *P. nemorosa* and *P. pseudosyringae*, is common at Sonoma Coast but absent at the Salt Point study location *(fig. 1*).

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Continued

Susceptibility to Sudden Oak Death in California Bay Laurel[1]

Brian Anacker,[2] Nathan Rank,[2] Daniel Huberli,[3] Matteo Garbelotto,[3] Sarah Gordon,[4] Rich Whitkus,[4] and Ross Meentemeyer[5]

Abstract

Sudden Oak Death, caused by the water mold *Phytophthora ramorum*, is a plant disease responsible for the death of 100s of thousands of oak and tan oak trees. California bay laurel (*Umbellularia californica*) has been shown to play a key role in *P. ramorum* inoculum build-up and subsequent spread to oaks. While bay laurel appears to vary in susceptibility to *P. ramorum*, little is known about the causes or extent of this variability. An understanding of such dynamics helps in identifying the limits of infection, dispersal, and impact of plant pathogens. In this research, we examine how bay laurel susceptibility to *P. ramorum* is related to bay laurel phenotype, genotype, and environment. Based on data from lab susceptibility trials and field infection data collected from 97 trees from 12 populations in Northern California, we found that lab lesion size and field infection levels varied significantly among both bay laurel trees and populations. The phenotypic trait of leaf area was significantly related to lab lesion size, where bigger leaves produced bigger lesions. Variability in lesion size produced in the lab and infection levels in the field were significantly related to AFLP markers, suggesting a genetic basis to resistance. We also identified markers associated with phenotypic traits putatively involved in conferring susceptibility, including leaf toughness and leaf water content. At the population level, environmental variability significantly explains susceptibility to *P. ramorum*. This work demonstrates how susceptibility to *P. ramorum* in bay laurel depends on genetic, phenotypic, and environmental traits, providing useful information for predicting risk of *P. ramorum* spread from bay laurel to oak and tan oak trees, an important consideration for controlling the spread of Sudden Oak Death.

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[2] Sonoma State University. mailto: brian.anacker@sonoma.edu, rank@sonoma.edu.

[3] UC Berkeley. mailto: huberli@nature.berkeley.edu and matteo@nature.berkeley.edu.

[4] Sonoma State University. mailto: sarahgordon17@aol.com and whitkus@sonoma.edu.

[5] University of North Carolina. mailto: Charlotte, rkmeente@email.uncc.edu.

Continued

Sudden Oak Death II

Continue

Tree Seedling Distributions Across a Gradient of *Phytophthora ramorum*-infected Coast Live Oak/Bay Forests[1]

Letty Brown[2] and Barbara Allen-Diaz[2]

Abstract

The effects of sudden oak death (SOD) on coast live oak/bay forest succession are still largely unknown. One scenario suggests that bay will become a greater component of the overstory in infected coast live oak-bay forests and that these communities will succeed to bay forests over time. We investigated tree seedling densities of coast live oak and bay in forty plots in eight sites over a three-year period across a gradient of SOD-infected oak woodland/bay forests. Classification and regression tree analysis (CART) and analysis of variance models were used to investigate a number of stand and landscape variables as predictors of seedling numbers over the infection gradient. Results indicate that a great deal of variability exists in seedling numbers for both oak and bay. Though other variables play smaller roles, site and year are the significant indicators of seedling densities for coast live oak, and site alone is the important indicator of bay seedling densities. Based on this study, we did not find bay seedlings in greater proportion to coast live oak seedlings in stands impacted by SOD. We do not believe that *P. ramorum* and the associated SOD complex is, at this time, causing succession towards bay-dominated forests. Rather the interplay between favorable weather years, herbivory, and other site factors will determine the competitive advantage of coast live oak or bay seedlings and the outcome for dominance of California's coast live oak/bay woodlands.

Keywords: Forest response, Quercus*, seedling dynamics, sudden oak death, succession,* Umbellularia.

Introduction

Sudden oak death (SOD), caused by *Phytophthora ramorum*, has killed thousands of oaks (*Quercus* spp.) and tanoaks (*Lithocarpus densiflorus*) in the coast ranges of California (Rizzo and Garbelotto 2003). The ecological implications of this pathogen on western forests, in terms of potential changes to forest structure and composition, are still not well understood. One scenario suggests that California bay laurel (*Umbellularia californica)* will become a greater component of the overstory in infected coast live oak-bay forests. McBride (1974) showed that in coast live oak/bay forests of the San Francisco Bay Area, coast live oak (*Quercus agrifolia*) naturally gives way to bay during normal succession with the removal of certain disturbances like livestock grazing. Thus, in forest stands where bay and coast live oak are codominant and coast live oak is killed by *P. ramorum*, bay should become a dominant component of the stand. Research has shown that in some areas of *P. ramorum* infection, the basal area of coast live oak has decreased by as much as 55 percent, while the BA of bay has increased from 25 percent to over 45 percent of the total basal area of the site (Brown and Allen-Diaz 2005). Other studies have shown substantial losses of coast live oak in terms of both basal area and numbers of

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[1] An abbreviated version of this paper was presented at the Sixth California Oak Symposium: Today's Challenges, Tomorrow's Opportunities, October 9-12, 2006, Rohnert Park, California.

[2] Graduate Student and Professor, respectively, Department of Environmental Science, Policy, and Management, Division of Ecosystem Sciences. University of California, Berkeley, CA 94720-3110.

individuals (Kelly and Meentemeyer 2002, McPherson and others 2005, Swiecki and others 2005).

Bay is not only the codominant tree with coast live oak in many areas of the coast range, it is also an important foliar host of the SOD disease (Davidson and others 2005). Mature bay trees exhibit high rates of *P. ramorum* sporulation, but as foliar and not stem hosts of the pathogen, they do not die from the infection. Therefore, bay is recognized as an important source of inoculum that contributes to oak mortality in coast live oak-bay woodlands. A relationship between bay and coast live oak mortality has also been demonstrated at the landscape scale in which density of bays was an important predictor of oak mortality (Kelly and Meentemeyer 2002). Swiecki and Bernhardt (2002) also described a spatial association between bay and *P.ramorum* infection on coast live oak.

Though mature bays may capture gap openings as coast live oaks are removed by SOD, the question remains whether and which species of tree seedling will be able to exploit the canopy openings created by the death of mature coast live oaks. Seedling survival in the understory is central to an understanding of forest succession as those trees capable both of surviving as understory plants and responding to release to reach overstory size will inevitably form a major portion of the dynamic forest community. Woody seedling germination and survival in oak/bay forests is a combination of a great number of factors. As well as water, light and nutrient needs critical for germination and growth, other factors such as distance from seed source, seedbed suitability, and predation at both the seed and seedling level are important. In this study, we compared environmental variables that addressed many of these factors and tested for differences between coast live oak and bay seedling densities in several *P. ramorum*-infected coast live oak/bay forests over a two- to three-year period.

Methods

Field Methods

We conducted this study at eight sites in the greater San Francisco Bay Area in California (Marin, Sonoma, and Contra Costa counties) on a mix of public and private lands. Sites were chosen to represent a gradient of visibly manifested signs of SOD infection, and were established to monitor vegetation change over this gradient (*fig. 1*). Skywalker (SKY) and both China Camp sites (CC1, CC2) show the greatest mortality from SOD while both Briones sites (EB1, EB2) show none. Olompoli (OLO), Fairfield Osborn Preserve (FOP), and Bouverie (BVR) are intermediate. At these eight 1-ha sites, five 0.08-ha plots were randomly located. In each plot, four 16 x 1m belt transects were established, radiating from the plot center stake and running in the cardinal directions. All seedlings <30-cm tall and <1-cm basal diameter were counted by species and transect (e.g., north, south, east, west) in the spring. These counts occurred in 2002, 2003, and 2004 for five of our sites (Skywalker, the China Camp sites, and the Briones sites), and in 2003 and 2004 for three of our sites (Olompoli, Fairfield Osborn, and Bouverie). We did not tag and track individuals over time.

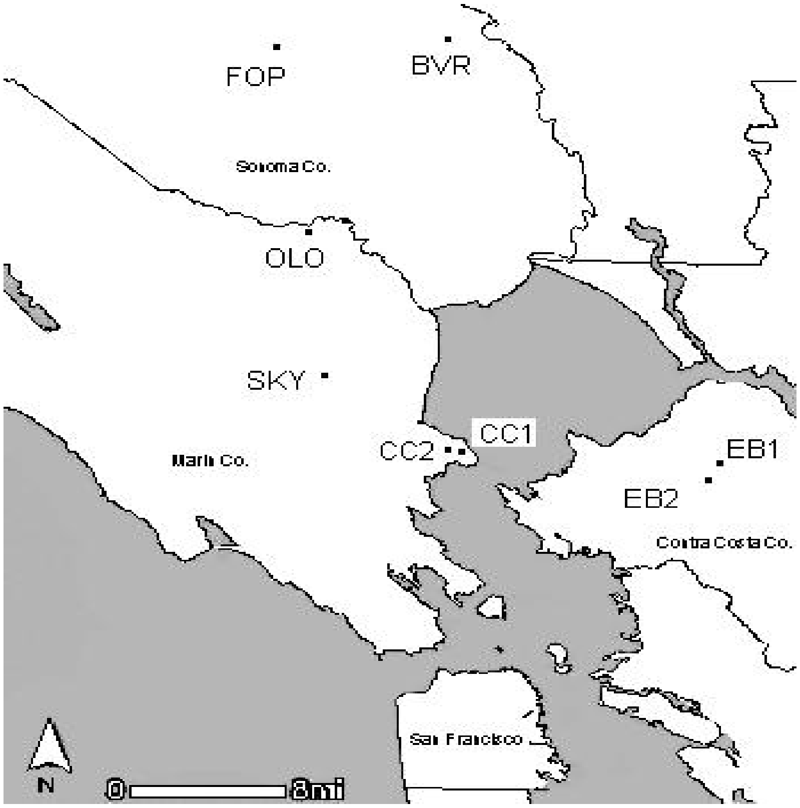

Figure 1—Map of study sites.

In each plot, many environmental variables were measured. Slope and aspect were measured at plot center. Basal area (BA) of all trees, snags and logs by species was recorded throughout the entire .08-ha plot. Log basal area was estimated at 1.37 m, based on the height of the remaining stump plus distance on the log to 1.37 m. Depths of litter and duff were measured to the nearest centimeter at 1, 11, and 16 meters along each transect, following Brown (1974).

Coarse woody debris (CWD) was measured using a variation on Waddell (2002), in which CWD was taken at each plot along the four 16-m transects for each piece of wood whose central axis crossed the tape and was larger than 8 cm in diameter. For each eligible piece of wood, the diameters of the largest and smallest ends (with a minimum of 8 cm) were recorded to the nearest 2.5 cm. The length of the log was recorded to the nearest 30 cm, not including the log portion smaller than 8 cm in diameter. To convert each piece of wood measured to a volume (m^3/ha), the following equation was used (from Waddell 2002):

$$\text{cubic volume of a log :} \quad V_{\text{ft}} = \frac{(\pi/8)(D_S^2 + D_L^2)l}{144}$$

where D_s and D_L are the diameters of the smallest and largest end of the log and l is log length. Comparisons between coarse woody debris loads were made based on these cubic volumes.

Leaf area index (LAI) was averaged from multiple readings taken in each plot in mid-late October. LAI data was collected from Skywalker, China Camp Miwok, China Camp Back Meadows, Briones Bear Creek, and Briones Alhambra in 2002, Olompoli, Bouverie, and Fairfield Osborne in 2003, and all sites in 2004. At each site, above canopy (A) and below canopy (B) readings were obtained using the LAI-2000 Plant Canopy Analyzer optical sensor (Li-Cor, Inc, Lincoln, NE). In accordance with LAI-2000 protocol, A readings were taken in a clearing, while B readings were taken manually at six different points beneath the canopy in each of the five plots at a site. Three readings were taken at each of six locations per plot and averaged.

Pathology data was taken in all plots in the spring of 2003 and 2004. Nine bay leaves (three leaves x three trees) were tested per plot. Leaf tissue was tested for presence or absence of *P. ramorum* using PCR methods (processed by Garbelotto lab, UC Berkeley).

Statistical Methods

An index of SOD impact was developed to create a ranking of SOD severity on our sites (Apigian 2005). To do this, we used PC-ORD to run a principle components analysis (PCA) (McCune and Mefford 1999) to construct a composite variable (based on PCA scores) to which we categorically assigned a SOD infection score for each plot (5 plots x 8 sites = 40 plots). We used five environmental variables as important indicators of SOD infection: percent of total basal area composed of dead coast live oak snags, percent of total basal area in live coast live oak trees, LAI, CWD volume, and percent of all coast live oak stems that were symptomatic of SOD (based on stems that exhibited seeping, that were found in plots that tested positive for *P. ramorum*). These variables were selected because they represent a range of impacts that SOD may have on a stand, as opposed to using any single metric. The variables used meet the assumptions of PCA (McCune and Grace 2002).

We used a classification and regression tree analysis (CART) to model relationships between tree seedling densities and landscape variables. CART models are developed by recursively partitioning the response variable into increasingly homogenous subsets based on critical threshholds in continuous or categorical variables (Crawley 2002). Tree-based models are graphically displayed so that one can follow the tree node through a series of binary splits on the predictor variable to an end node. We used a regression tree analysis with tree seedling density as our output variable. The estimate for all observations that follow the same lineage of branching to an end node is given by the mean x-value for that set of observations.

The Tree Model function in S PLUS 6.1 (SAS 2002) was used for our analysis. After developing species-specific models for different years separately, a model was developed that pooled all years together, using density of seedlings as the dependent variable and the corresponding values of each landscape or stand variable for model development. Default settings were used. The following equation shows the independent variables used in these final models, where the dependent variable was either coast live oak or bay seedling density:

- Seedling density = f (LAI, BA live coast live oak m2/ha, BA live bay m2/ha, duff depth, litter depth, CWD m3/ha, northness index, slope, plot-based SOD index, site, year)

The northness index was derived using the following equation, starting with aspect in radians: Northness = cosine(aspect) . The plot-based SOD index was the index derived from PCA scores.

To prune the CART trees, the cost-complexity setting was employed which generated a table that showed how the model deviance decreased as the number of nodes changed (Crawley 2002). Using these data, a deviance of 0.1 was chosen. This number encompassed the largest jumps in deviance and was used for all models.

Additionally, ANOVA in S PLUS 6.1 (SAS 2002) was employed using independent variables identified by the first and second runs of CART to determine the degree of significance among plots.

Results

We found that large amounts of spatial and temporal variability existed in seedling densities (*table 1*). Results indicated that coast live oak, bay, and toyon (*Heteromeles arbutifolia*) were consistently the predominant woody species represented in the seedling layer. There were few seedlings found of the other tree species in the plot including black oak (*Quercus kellogii*), Pacific madrone (*Arbutus menziesii*), Oregon oak (*Quercus garryana*), Big leaf maple (*Acer macrophyllum*), California buckeye (*Aesculus californica*), and Douglas fir (*Pseudotsuga menziesii*). Certain sites tended to have more total seedlings (*table 1 and 2*), as well as more seedlings of certain species. The two China Camp sites had the highest mean densities of seedlings (*table 2*); however these high numbers were largely driven by toyon which comprised 97 and 99 percent of site totals in 2003 (*table 1*).

Skywalker consistently had the highest numbers of coast live oak seedlings; it had over 20 times more coast live oak seedlings than other sites in 2002, and had higher numbers than all other sites in the other two years of the study. Bouverie, the second highest-producing site for coast live oak seedlings, had 5.5 times more seedlings in 2003 and 2004 than all other sites, besides Skywalker. Bay, too, exhibited a large variation in mean seedling densities among sites. Briones Bear Creek had consistently higher densities than all other sites; it had up to 33 times more bay seedlings than the China Camp sites and Fairfield Osborn.

Table 1—*Total number of seedlings by species per site including coast live oak (Quag), bay (Umca), toyon (Hear), and 'other' species in 2002, 2003, 2004. 'Other' includes black oak (Quercus kellogii), Oregon oak (Q. garryana), Big leaf maple (Acer macrophyllum), Pacific madrone (Arbutus menziesii), California buckeye (Aesculus californica) and Douglas fir (Pseudotsuga menziesii). Seedling numbers were counted along a total of twenty 16 m^2 belt transects per site (320 m^2 total area).*

Site	**Sum (‘02) Qu ag**	**Sum (‘03) Qu ag**	**Sum (‘04) Qu ag**	**Sum (‘02) Um ca**	**Sum (‘03) Um ca**	**Sum (‘04) Um ca**	**Sum (‘02) He ar**	**Sum (‘03) He ar**	**Sum (‘04) He ar**	**Sum (‘02) Other**	**Sum (‘03) Other**	**Sum (‘04) Other**	**Grand Total**
Sky	349	177	34	110	97	61	0	0	0	0	0	0	**828**
CCMiwok	24	20	13	12	14	12	33	1100	20	0	0	0	**1248**
CCBackMdw	2	3	3	6	5	1	19	742	59	0	0	0	**840**
BrionesAlh	13	7	1	69	60	66	1	0	0	0	0	0	**217**
BrionesBrCk	0	22	23	246	190	239	8	18	7	1	0	0	**754**
Olompoli	*na*	19	20	*na*	90	83	*na*	15	4	*na*	4	6	**241**
Bouverie	*na*	147	37	*na*	123	110	*na*	45	25	*na*	24	9	**520**
FOP	*na*	42	27	*na*	19	16	*na*	1	1	*na*	6	5	**117**
total	**388**	**437**	**158**	**443**	**598**	**588**	**61**	**1921**	**116**	**1**	**34**	**20**	**4765**

Table 2—*Average seedling density (all species) per site. For sites Skywalker, China Camp Miwok, China Camp Back Meadows, Briones Alhambra, and Briones Bear Creek, these values represent densities from '02-'04. For sites Olompoli, Bouverie, and Fairfield Osborn, values represent only '03 and '04 numbers. In the statistical differences column, sites w/the same symbol (+, ++, and –) are not statistically different from one another.*

Site	**mean seedlings per m^2**	**n**	**SE**	**Statistical Differences**
Sky	1.38	15	0.26	+
CCMiwok	2.08	15	0.72	++
CCBackMdw	1.39	15	0.66	+
BrionesAlh	0.37	15	0.03	-
BrionesBearCrk	1.32	15	0.17	+
Olompoli	0.72	10	0.08	+
Bouverie	1.32	10	0.17	+
FOP	0.30	10	0.08	-

Table 3—*Total seedlings counted at each site, by year.*

Site	**2002 total**	**2003 total**	**2004 total**
Sky	459	274	95
CCMiwok	69	1134	45
CCBackMdw	27	750	63
BrionesAlh	83	67	67
BrionesBearCrk	255	230	269
Olompoli	*na*	128	113
Bouverie	*na*	339	181
FOP	*na*	68	49
Total	893	2990	882

Principal Components Analysis indicated that the first axis was the best synthesis of the variables potentially associated with SOD. The eigenvalue of 3.724 was much greater than all other axes indicating that axis 1 was the only significant axis for interpretation (McCune and Grace 2002). This axis represents a strong SOD gradient from high SOD impact (low proportion of live oaks, high proportion of dead oaks, high light penetration, high woody debris volume, and high incidence of SOD) to low impact of SOD. We adjusted the axis scores by taking the inverse of the PCA values so that the index would run from least affected to most affected plots. We then took the absolute value of the PC 1 axis values, setting the least affected plot to 1 with the most affected plot receiving a score of 8.89. These adjustments did not change the scale of the original PCA axis and were done simply to ease interpretation and analysis.

Coast Live Oak

The model included 983 coast live oak seedlings recorded over three years. CART analyses showed that site and year were the most important variables explaining the number of coast live oak seedlings. Skywalker was initially separated from the other sites, and then Bouverie (*fig. 2*). Both of these sites had high mean seedling densities while the other sites had lower mean densities (0.86 seedlings/plot). Seedling densities varied greatly by year (*table 1*) and the CART analysis validated the importance of the year effect. For example, Skywalker (*fig. 2*) had the highest mean seedling densities in 2002 (17.45 seedlings/plot), followed by 2003 (8.85 seedlings/plot), and the lowest density in 2004 (1.70 seedlings/plot).

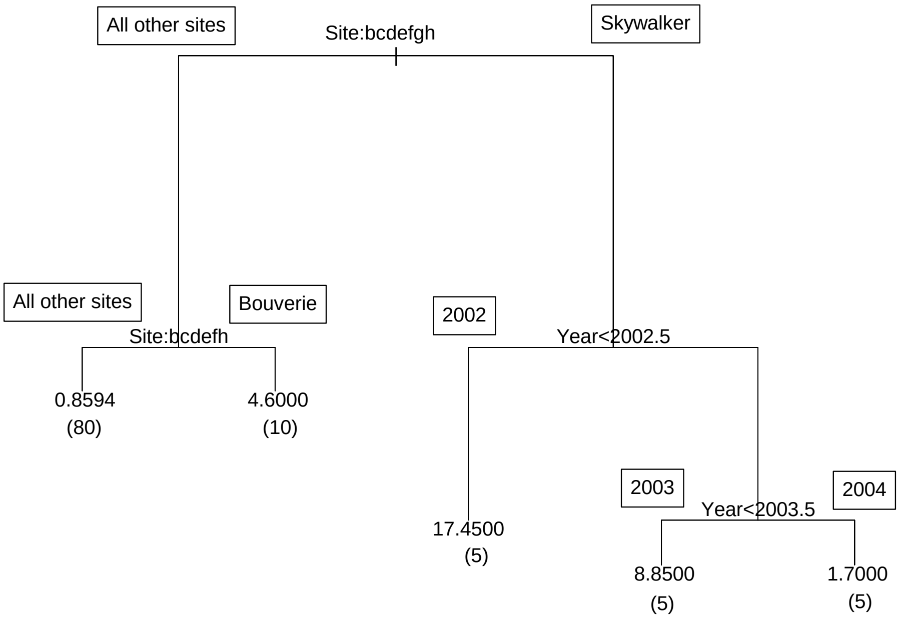

Figure 2—Final CART model chosen for coast live oak. Numbers in parentheses below the end node represent the number of plots in each subset.

Figure 3, below, shows that after excluding site and year from the CART model, northness and bay basal area were the most important variables predicting coast live oak seedling densities. The highest mean coast live oak seedling density (15.71 seedlings/plot) occurred on south facing slopes, in which bay basal areas were >0.79 m^2/ha. For the remaining plots, live bay basal area was again an important predictor of coast live oak seedling density. On these sites, on more north-facing slopes, a lower live bay basal area (<0.52 m^2/ha) and a lower SOD index (<1.93) predicted higher seedling densities (4.160 seedlings/plot) compared to plots with higher SOD index (1.01 seedlings/plot).

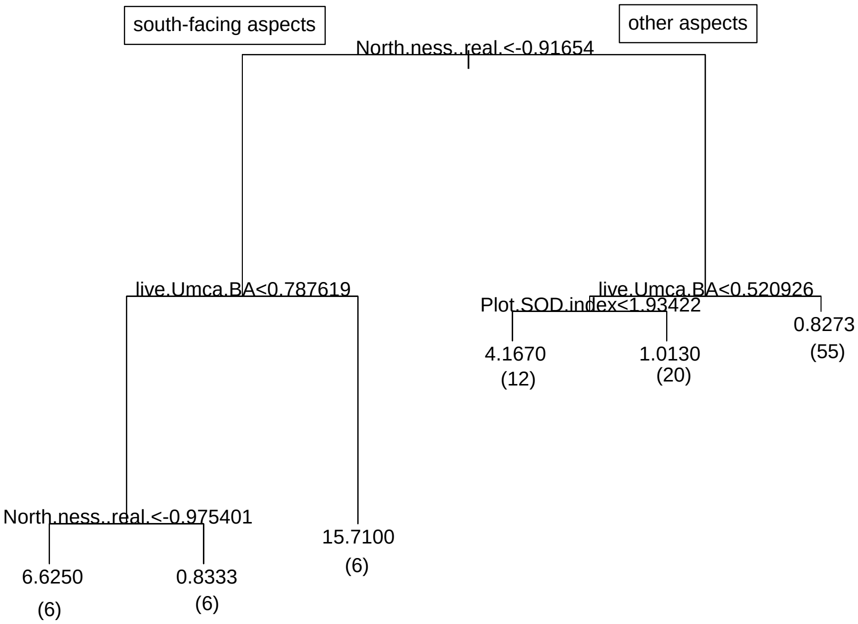

Figure 3—Second CART model without site and year. Northness, live bay basal area, and SOD index were the most important predictor variables for coast live oak seedling numbers. Numbers in parentheses below the end node represent the number of plots in each subset.

Table 4 shows ANOVA results run on the important variables identified by the first and second models of CART. As expected, both site and year are significant predictors of seedling numbers of coast live oak. There is also a significant interaction between site and year, indicating that these two variables are not consistent, that is they do not vary together in the same way (*see table 1*). The remaining environmental variables were not significant.

Table 4—*ANOVA results for coast live oak seedling densities over the 2002-2004 time period. Variables chosen for the model were from CART models (fig. 2 and 3).*

	Df	Sum of Sq	Mean Sq	F Value	Pr(F)
Site	7	982.4363	140.348	14.60511	0.0000000
Year	1	184.5043	184.5043	19.20017	0.0000331
Northness	1	5.0635	5.0635	0.52693	0.4698722
liveUmcaBA	1	5.3601	5.3601	0.5578	0.4571869
plotSODindex	1	0.676	0.676	0.07035	0.7914614
Site:Year	7	514.7816	73.5402	7.65285	0.0000004
Residuals	86	826.4184	9.6095		

Bay

The bay model analyzed 1,629 seedlings as response variables over the three-year period. The final model deviance was set to 0.1, and showed that site, northness, and duff depth had the highest explanatory value (fig. 4). Of these, site was the most important, separating Briones Bear Creek from the other sites, and then separating the two China Camp sites and Fairfield Osborn Preserve, with a lower mean seedling density (0.53 seedlings/plot) from the other sites (fig. 4). At the next node, average duff depth dictated whether the mean bay seedling density was 7.25/plot (less duff depth), or 3.79/plot (higher duff depth). For Briones Bear Creek, northness was the key determinant of seedling density. Lower northness determined a higher mean (17.5 seedlings/plot), while higher northness meant a lower mean density of bay seedlings (7.08 seedlings/plot).

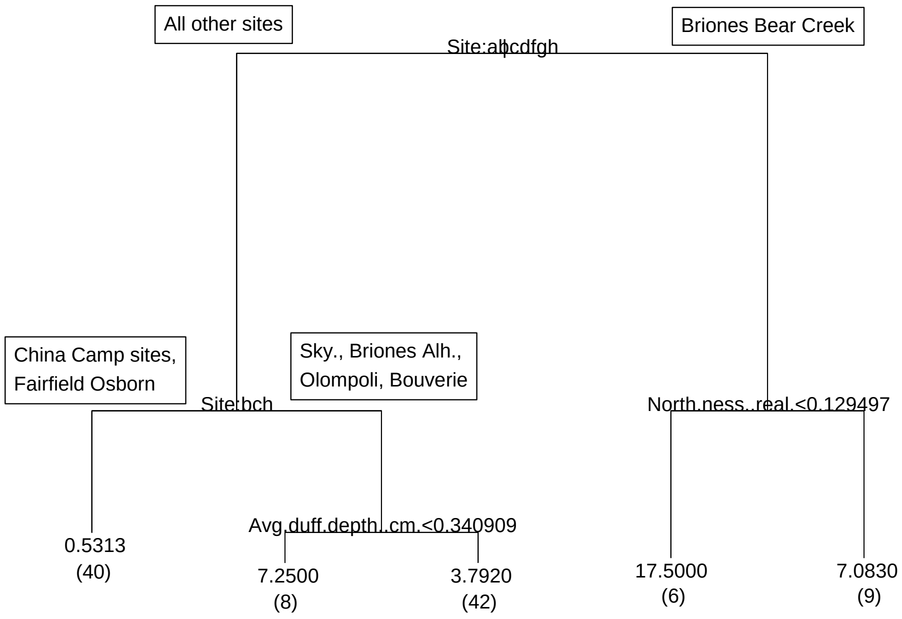

Figure 4—CART model chosen for bay. Numbers in parentheses below the end node represent the number of plots in each subset.

As with coast live oak seedling analysis, a second CART model was constructed eliminating site, northness, and average duff depth from the model in order to explore further important relationships (*fig. 5*). LAI was the most important variable predicting bay seedling density, showing that more seedlings occur in areas with higher LAI (and thus more shade). The highest mean seedling density (17.5/plot) represented sites whose LAI value was higher than 2.98, and whose bay basal area was higher than 0.79 m^2/ha but less than 1.03 m^2/ha.

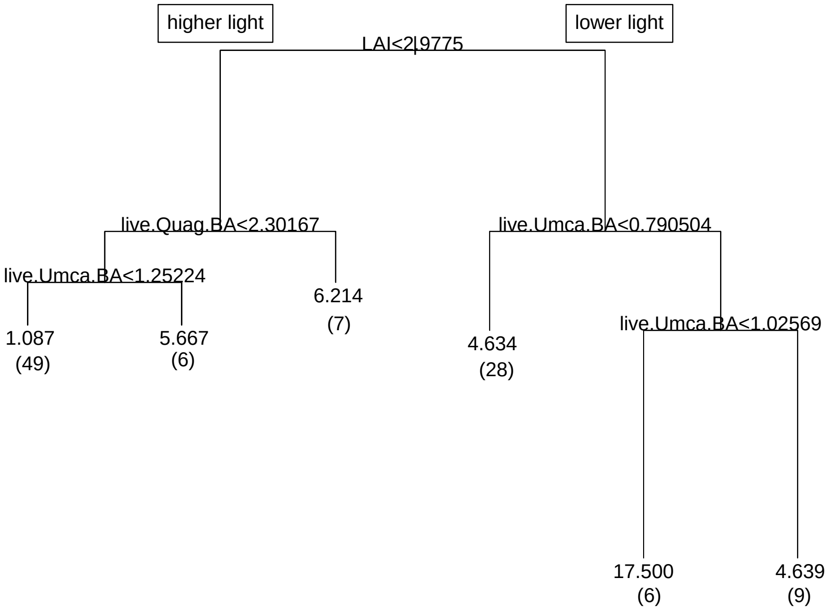

Figure 5—CART model chosen for bay, run without the variables in the first model. Here LAI, live coast live oak basal area, and live bay basal area are the most important predictors of densities of bay seedlings. Numbers in parentheses below the end node represent the number of plots in each subset.

Table 5 shows ANOVA results run on the variables identified by the first and second models of CART. As expected, site and LAI are significant predictors of seedling numbers of California bay. The remaining environmental variables were not significant.

Table 5—*ANOVA results explaining variability in bay seedlings over the 2002-2004 time period. Variables in the model were those identified by the two CART models run.*

	Df	Sum of Sq	Mean Sq	F Value	Pr(F)
Site	7	1317.229	188.1756	23.25514	0
Duffdepth	1	1.625	1.6248	0.2008	0.655133
Northness	1	5.678	5.6784	0.70175	0.404368
LAI	1	32.873	32.8734	4.06257	0.046761
liveQuagBA	1	0.003	0.0033	0.0004	0.984036
liveUmcaBA	1	29.911	29.9115	3.69652	0.057619
Residuals	92	744.444	8.0918		

Discussion

The effects of SOD on coast live oak/bay forest succession are still largely unknown, particularly in these early stages of the disease. McBride (1974) suggested that coast live oak/bay communities, in the absence of disturbances like livestock grazing, would naturally succeed to bay forests over time. With the death of coast live oak, successional processes toward bay could be accelerated.

Our results indicate that a great deal of spatial and temporal variability exists for both coast live oak and bay seedlings. Site is the most important indicator of seedling density for both our coast live oak and bay models, possibly indicating that environmental factors accounting for the variance in seedling densities were not measured in this study.

Year is a significant indicator of seedling density in the coast live oak model but not in the bay model. This finding is commensurate with the literature, as oaks are known masting species and therefore acorn production varies between years and is cyclic, with large-scale weather patterns influencing production levels (Koenig and others 1996). The lack of a year effect on bay seedlings in our models suggests that bays do not appear to be as subject to temporal asynchrony as the oaks.

One environmental variable was statistically significant in the ANOVA models. We found leaf area index to be a predictor of bay seedling densities, but not of coast live oak seedling densities. The CART model demonstrates that bay seedling densities are higher in areas with less light. This finding could be an artifact of lowered light levels beneath mature bay trees, indicating that distance to seed source is an important variable for bay seedlings, rather than light levels per se. Further, mature bay basal area was almost significant at the 95% level in the bay ANOVA model. However, either of these scenarios is important in predicting seedling dynamics in gap openings produced by SOD, as it may mean that bay seedlings are more limited than oak seedlings by light levels or distance to seed source.

Little literature exists on bay seedling requirements to support or refute these claims. Mature bays are generally classified as shade-tolerant, but tolerance levels are not well defined (USDA 1965). McBride showed that bay seedlings can invade open grasslands and brushlands in the Berkeley hills (McBride 1974); similar capabilities were observed in the Santa Cruz mountains (Unsicker 1974).

Particularly amidst concern that certain oak species are not replacing themselves, several studies have evaluated shade-tolerance levels in coast live oak seedlings. Coast live oak seedlings are exceptionally shade-tolerant compared to seedlings of some other California oak species, and are able to maintain high photosynthesis capacities and root elongation in low light (Callaway 1992). Many studies have found that coast live oak seedlings are spatially associated with shrublands (McBride 1974, Muick and Bartolome 1987, Callaway and D'Antonio 1991, Callaway and Davis 1998). One study showed that seedling survival is enhanced by artificial shade (Muick 1991). However, whether this is due to shade tolerance factors (i.e., moisture requirements) in coast live oak seedlings, or other factors such as seedbed suitability or protection from herbivory is unclear.

Other parameters will be important in determining the successional outcome at any coast live oak/bay site and future studies should account for these. Bay seedlings can be foliar hosts of *P. ramorum* which may affect leaf retention in seedlings as it does in mature bays (Davidson and others 2005), potentially affecting bay seedling survival. Both bay and coast live oak seedlings are susceptible to herbivory from a variety of vertebrate and invertebrate grazing animals. Tyler and others (2002) found that seed predation and herbivory by small mammals significantly reduced coast live oak seedling recruitment in a study conducted at the Sedgwick Reserve in Santa

Barbara County. Both coast live oak and bay seedlings are palatable to deer (Sampson and Jesperson 1963, McBride 1974). An additional factor for future investigation is an analysis of whether CWD will provide refugia for oak seedling survival, similar to Callaway and D'Antonio's (1991) determination that shrubs facilitate coast live oak seedling survival.

Future studies should include measurements of individual seedling survival and growth rates as seedling growth rates vary. Some studies suggest that bay seedlings grow fast, attaining up to 30-cm growth per year on favorable sites (USDA 1965). One study on restoration of coast live oak found that in irrigated tree shelters (a favorable site), coast live oak may attain 38-cm growth per year (Plumb and De Lasaux 1996), but under normal field conditions coast live oaks were found to grow much more slowly often persisting at heights of approximately 10 cm for many years (Muick 1997).

Conclusions

In these early stages of the disease, we do not believe that *P. ramorum* and the associated SOD complex is accelerating successional processes toward bay-dominated forests. In our study, numbers of coast live oak and bay seedlings, evaluated over three years in the early stages of SOD, did not appear to be affected by the presence of SOD. Our gradient of infection from little-to-no presence of *P. ramorum* in Briones sites to considerable presence and visible effects of oak die-off at Skywalker and China Camp did not correlate with coast live oak or bay seedling numbers. However, seedling survival is only one part of this picture. Recruitment into saplings, pole and, finally, tree-sized classes are important components of stand succession. The temporal variability of SOD pressure is also important. Thus the interplay between favorable weather years, herbivory, site factors, and variation in SOD pressure will determine the competitive advantage of coast live oak or bay seedlings and the outcome for dominance of California's coast live oak/bay woodlands.

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Continue

Human Activity and Spread of the Pathogen That Causes Sudden Oak Death[1]

Hall Cushman[2] and Ross Meentemeyer[3]

Abstract

A striking consequence of globalization is the tremendous influx of infectious diseases and invasive, non-natives species worldwide. One invader of great concern is the fungus-like pathogen, *Phytophthora ramorum*, which causes a devastating forest disease known as Sudden Oak Death (SOD) in many coastal regions of California and Oregon. In addition, *P. ramorum* has been found in nurseries and managed landscapes throughout Europe (11 countries so far) and recent laboratory studies have indicated that numerous oak species in the eastern United States are extremely susceptible to attack by the pathogen, should it reach these areas in the future. Here, we evaluate the influence of human activity on the distribution of this pathogen at three spatial scales in California. At the local scale, we found that *P. ramorum* was significantly more common in soil found on hiking trails at Fairfield Osborn Preserve than from adjacent areas off trail. At the landscape scale, forests on public lands in eastern Sonoma County open to recreation had significantly higher proportions of diseased host trees than those on private lands. And at the regional scale, forested areas in northern and central California surrounded by large human populations were significantly more likely to have infected host trees. Collectively, these findings suggest that humans are important dispersal agents of a destructive pathogen and promote its spread. Efforts to address this epidemic may thus require aggressive management of human activity, which could be logistically and politically difficult to achieve.

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[2] Sonoma State University. e-mail: cushman@sonoma.edu.

[3] University of North Carolina, Charlotte. e-mail: rkmeente@email.uncc.edu.

Continue

Effects of Recreation on the Dispersal of *Phytophthora ramorum*[1]

Michelle Cooper[2] and Hall Cushman[2]

Abstract

Although outdoor recreation is often viewed as having minimal impacts on protected wildlands, a growing number of studies have shown that hiking trails can serve as corridors for the spread of exotic plant species. Very little research has focused on recreation as a means of spread for plant pathogens but here, we present research that links two forms of recreation (hiking and mountain biking) with the dispersal of an exotic forest pathogen, *Phytophthora ramorum*, which causes the disease known as Sudden Oak Death. By sampling soil collected from the shoes and tires of visitors entering and exiting protected wildlands, we found that 7% of visitors entered the site with viable pathogen on their shoes and tires, and 23% carried it out with them. Although hikers and bikers did not differ significantly in their capacity to transport *P. ramorum*, there was a trend indicating that during dryer conditions, the further a person traveled along a trail, the more likely they were to pick up the pathogen. Lastly, although our data show that humans can disperse *P. ramorum*, the temporal window for doing so is constrained, as the pathogen could not be cultured from soil on hikers shoes after 24 hr, although this time was extended to at least 72 hr if the soil on shoes remained moist. Collectively, our results suggest that recreation in protected areas can lead to dispersal of the pathogen that causes Sudden Oak Death. However, because *P. ramorum* is sensitive to desiccation, human dispersal may be limited to situations where the pathogen remains moist. These include further spread of the pathogen during individual visits to already infected areas and movement of the pathogen to previously uninfected areas when visitors move rapidly from one region to another, especially when shoes and tires are stored in moist conditions.

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[2] Sonoma State University, Department of Biology. e-mail: michellezmail@yahoo.com and cushman@sonoma.edu.

Continue

GIS-Based Epidemiological Modeling of an Emerging Forest Disease: Spread of Sudden Oak Death Across California Landscapes[1]

Rich Hunter[2] and Ross Meentemeyer[3]

Abstract

The number of emerging infectious diseases are thought to be increasing worldwide - many of which are non-native, invasive plant diseases in forest ecosystems. A predictive understanding of invasion processes is necessary to manage and prevent further spread, especially in complex spatially heterogeneous landscapes. Mathematical modeling of susceptible-infectious transitions in plant epidemics often incorporate spatial dynamics, but are rarely applied in a GIS to real-world wildland landscapes. In this paper, we present and evaluate a GIS-based epidemiological model of the spreading forest pathogen *Phytophthora ramorum*, which is causing the devastating forest disease known as Sudden Oak Death. First, we describe a generic mathematical model for a susceptible-infectious epidemic that simulates spatial and temporal patterns of disease spread on a weekly time step for application at large spatial scales. Next, we describe how data from field and lab studies were used to parameterize the driving system variables, including daily rainfall and temperature, host abundance and susceptibility, human density, and dispersal characteristics. The parameterized model was implemented (1990-2005) in a GIS to simulate disease spread across California at a spatial resolution of 250 x 250 meters. We evaluated model performance in the GIS by examining the correspondence between predicted patterns of disease spread and over 1000 geo-located field observations of disease presence. Additionally, we examined the nature of prediction errors by ecoregion, vegetation composition, and climate. The model predicts almost 80% of the spatial variability in current patterns of disease spread and identifies numerous oak woodland systems at high risk of infection. We've found the application of epidemiological models to realistic landscapes in a GIS can allow for a rigorous validation of model performance using geo-located field data of disease presence and can be used as an effective management tool to identify actual landscapes at high risk to disease spread.

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[2] Sonoma State University. e-mail: rich@talonassociates.net.

[3] University of North Carolina, Charlotte. e-mail: rkmeente@email.uncc.edu.

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Long-Term Change in Oak Woodlands and Its Influence on a Forest Disease[1]

Ross Meentemeyer[2] and Hall Cushman[3]

Abstract

Land-use practices to sustain expanding human populations have resulted in dramatic alterations of forested ecosystems worldwide. One potential consequence of land-use change is the spread of infectious disease. In this research, we investigated patterns of human-related land-cover change between 1942 and 2000 and examined whether or not changes have led to conditions that promote the establishment and spread of the invasive pathogen *Phytophthora ramorum*, causal agent of the destructive forest disease Sudden Oak Death. We established 102 field sites randomly located within a 275 km2 region of Sonoma County, CA comprised of several land cover types. Within a 150 m radius area around each site, we mapped fine-scale changes in land cover in a GIS using 1942 and 2000 imagery. We found that woodland area increased by 25% from 1942 to 2000, while grassland and chaparral decreased in area by 34% and 49% respectively, and development increased by 1105%; mean size of woodland patches increased by 51% and number of woodland patches decreased by 41%. To examine if these changes influenced the establishment of *P. ramorum*, we sampled *P. ramorum* infection level on host species and measured woody species abundance within each 150 radius area in spring 2005. Multiple regression analyses showed that density of the host bay laurel (an important carrier of the disease) was positively related to woodland cover change. Also, there were a greater number of bay trees showing symptoms of *P. ramorum* in areas that have increased in woodland. We hypothesize that these increases in woodland density and expansion into grasslands and shrublands facilitates spread of *P. ramorum* by increasing contagion of host and increasing shading and moisture levels. Understanding the influence of land cover change on disease spread is critical for informing land management and preventing intensification and spread of destructive pathogens.

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[2] University of North Carolina at Charlotte. e-mail: rkmeente@email.uncc.edu.

[3] Sonoma State University. e-mail: cushman@sonoma.edu.

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Gap Dynamics in Oak Woodlands Across a Gradient of Disturbance[1]

Tim De Chant,[2] Maggi Kelly,[2] and Barbara Allen-Diaz[2]

Abstract

Sudden oak death (SOD) is a disease of epidemic proportions, sweeping through many coastal hardwood forests in California. Since 1999, *P. ramorum* has produced overstory mortality in China Camp State Park (CCSP) and the surrounding open space, creating a number of gaps which effectively alter the structure of the forest. In the following year, ADAR high-resolution (1 m) multispectral imagery for CCSP was acquired. We classified this existing imagery to identify gaps within the forest mosaic. Once the gaps were identified, they were measured for area, perimeter, and Euclidean nearest neighbor. We then compared these spatial measures of variation to temporal ones, creating a time-sequence of gap formation and the resulting gaps' closure or persistence. Between 2000 and 2001, 910 gaps within China Camp contained one or more trees dead from *P. ramorum*. Of those, the majority decreased in both size and perimeter, and the distance between them grew. Those that increased in size, however, were smaller on average than those that decreased, a potential consequence of the spatial distribution of SOD. This research is still in its early phases but provides insight into changes in the canopy structure at China Camp following *P. ramorum* mortality.

Keywords: Multi-temporal, object-based image analysis, P. ramorum, Quercus*, remote sensing, sudden oak death.*

Introduction

The forest pathogen *Phytophthora ramorum* has had a significant impact on the forests of central coastal California. Since it was first reported in 1995, it has killed hundreds of thousands of trees, including coast live oak (*Quercus agrifolia*), tanoak (*Lithocarpus densiflorus*), and California black oak (*Q. kelloggii*) (Rizzo et al. 2002). While the pathogen can take anywhere from 2 to 20 years to kill an individual tree (McPherson et al. 2005), the steady final decline of the trees has created new openings throughout the affected forests. The pathogen also causes rapid foliar die-back when a canker infection overwhelms the tree, giving it the name "Sudden Oak Death" (Rizzo and Garbelotto 2003). This swift browning and eventual defoliation of the crown allows the use of remote sensing in the detection of this decline and the tracking of the mortality caused by its progression through the forest.

Remote sensing of forest diseases is a relatively new but developed field (Franklin and others 2000, Pinder and McLeod 1999). Much of the work has been done on coniferous forests, and there have been a few studies that have looked at pathogens in broad-leaved stands (Everitt and others 1999, Gong and others 1999, Liu and others 2006b). Sudden oak death, a relatively new disease, lends itself well to multi-temporal study via remote sensing. The rapid foliar death (two to four weeks)

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[2] Graduate Student, Associate Professor, and Professor, respectively, Department of Environmental Science, Policy and Management, University of California, Berkeley, CA 94720. e-mail: dechant@nature.berkeley.edu, mkelly@nature.berkeley.edu, ballen@nature.berkeley.edu.

(Davidson and others 2003), means the annual mortality caused by the pathogen is readily apparent from the air. Researchers noticed the progression of this mortality, and work commenced shortly after the pathogen started sweeping through stands. Early research focused on monitoring the affected forests (Kelly and McPherson 2001, Kelly and Meentemeyer 2002) with later efforts working on increasing the accuracy of correctly identifying dead trees (Kelly and others 2004, Liu and others 2006b, Sun and others 2005).

Remote sensing has also progressed since work on SOD began, particularly with the broader use of object-based image analysis (OBIA). In the past 10 years, a number of factors have conspired to bring about the development of OBIA (Hay and others 2005). First, as spatial resolution in imagery has become smaller, individual pixels may no longer be representative of one or more objects but rather a component part of a target feature. Additionally, as image resolution increases, it becomes increasingly easier for humans to decipher individual smaller-scale objects on the ground. This has inspired the development of programs that can assemble the pixels of an image into discreet objects. Finally, as computers have become more powerful, the processing of high-resolution imagery with computationally intensive OBIA methods has become faster and more accessible. OBIA has seen broad application in the field of environmental remote sensing. As many types of environmental data are spatially dependent, these methods are a natural fit. In Siberia, OBIA has been used to classify areas of deforestation by incorporating proximity to linear features such as roads in the classification (Hese and Schmullius 2006). In New Mexico, object-based methods have aided in mapping shrub encroachment and its intensity. This was accomplished by segmenting the image at varying scales, identifying individual shrubs at finer scales, and then using that data to determine shrub density at coarser scales (Laliberte and others 2004). In this case, OBIA is particularly suited to identifying dead trees in the forest canopy. By segmenting an image into discreet objects, we can not only identify the dead trees, but also outline the extent of their reach.

Sudden oak death has affected coast live oak trees with larger stem diameters more than smaller ones, a characteristic of the disease that has pushed the size distribution of affected populations down. As a result, we may see a downward shift in the age distribution due to the appearance of new seedling cohorts (McPherson and others 2005). Previous work on gap dynamics in California oak woodlands suggests that oaks may need a shrub-dominated stage for successful recruitment (Callaway and Davis 1998), but few studies to date have examined such events following SOD (see Brown and Allen-Diaz in this publication for an example).

While seedling recruitment may be the direction of future events, the crown structure of the remaining overstory trees will likely be impacted on a more immediate time scale. Most research into gap dynamics in oak woodlands has examined recruitment (Asbjornsen and others 2004b, Callaway and Davis 1998) and microclimatic effects (Asbjornsen and others 2004a) with few focusing on changes in canopy structure (Clinton and others 1993). With SOD removing larger trees from the canopy in a spatially contagious pattern (Kelly and Meentemeyer 2002), the openings are concentrated in some areas while relatively sparse in others, creating a gradient of disturbance. In this project, we sought to explore changes in the forest canopy at China Camp following mortality caused by *P. ramorum* at both the landscape and individual gap scales. Specifically, we used object-based image analysis to delineate, classify, and structurally quantify changes in canopy gaps caused by *P. ramorum* in the years 2000 and 2001.

Figure 1—At left: A sudden oak death (SOD) caused canopy gap at China Camp. At right: A healthy canopy at China Camp.

Study Site

The study area for this project is a forested peninsula in eastern Marin County. Jutting out into San Pablo Bay, the woodlands on the peninsula are managed in the northwest by Marin County Open Space as San Pedro Ridge Reserve, in the southwest by the City of San Rafael as Henry A. Barbier Park, and in the east by the California State Parks as China Camp State Park. While under separate jurisdictions and different official names, these three areas are commonly referred to as China Camp. A large portion of the open space on the peninsula features near even-aged stands containing *Q. agrifolia*, *Q. kelloggii*, and *Q. lobata* along with *Arbutus menziesii* and *Umbellularia californica*. Of these, *Q. lobata* is the only non-host species for *P. ramorum*. These stands are spread across a landscape with moderate to steep topography rising from sea level to over 300 m in elevation.

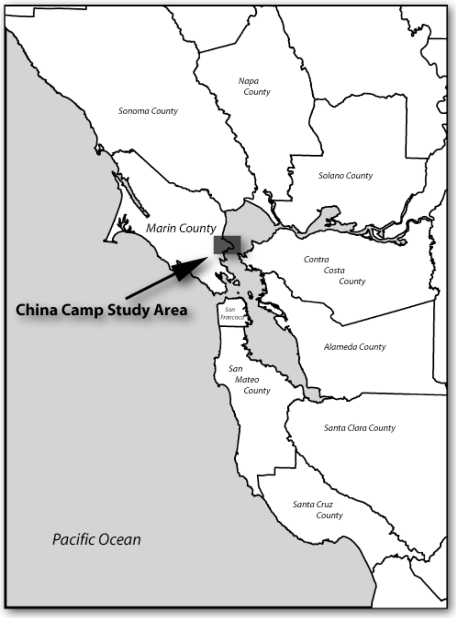

Figure 2—The China Camp study area is located in Marin County on the western shore of San Pablo Bay.

Methods

We acquired digital imagery for China Camp (*fig. 3*) annually from 2000 to 2003 through private contractors (Positive Systems, Inc. and ARINC, Inc.). In this study, we focused on imagery from 2000 and 2001. The imaging system was an ADAR 5500 that has an SN4, 20 mm lens with four mounted cameras of four corresponding spectral bands (Blue: 450-550 nm, Green: 520-610 nm, Red: 610-900 nm, and Near Infrared (NIR): 780-920 nm). The aircraft was flown at an average altitude of 675 m, giving each 1,000 x 1,500 m frame an average ground spatial resolution of 1 m. Each frame has 35 percent side- and 35 percent end-lap. The imagery used in this study was acquired on March 30, 2000, and May 5, 2001, both to reduce the confusion between dead trees and California buckeye, a summer deciduous tree, and to capture the springtime canopy cover change caused by SOD.

The frames for each year were mosaicked and georeferenced using a 15-cm resolution digital orthophotograph of the whole county provided by the Marin Municipal Water District. Positive Systems registered each year to an accuracy of 0.305 m. Further registration was performed to minimize inter-annual variations according to Liu and others (2006a). Inter-annual (2000-2001) RMSE was 1.83 m.

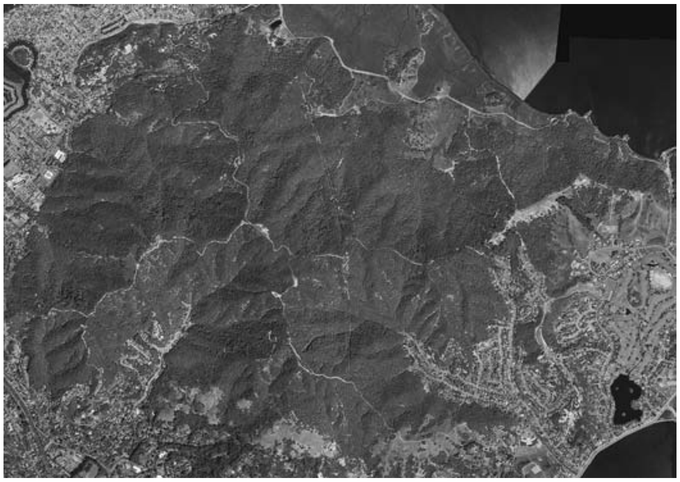

Figure 3—RGB-NIR image of China Camp study area in 2001. The City of San Rafael borders the east, west, and south, and San Pablo Bay borders the northern part of the site.

Enhancement and Segmentation of the Imagery

A number of indices and enhancements were applied to the mosaicked and registered images using ERDAS Imagine software (ERDAS 1999). Of these, three were useful: Normalized Difference Vegetation Index (NDVI), Kauth-Thomas Tasseled Cap, and intensity, hue, and saturation (IHS). The first two, NDVI and Tasseled Cap, were originally developed for Thematic Mapper data from the Landsat satellites (Crist 1985), but ADAR's similarity in spectral resolution allowed us to employ them. The last enhancement, IHS, simply recodes the original NIR-red-green-blue image into intensity-hue-saturation, another method for storing and representing image data. All of these layers, including the original 4-band raw imagery, were then loaded into Definiens Professional 5.0 (Definiens 2006), an object-based image analysis software package also known as eCognition.

The eCognition software package takes pixels in the images and pairs them with similar pixels, forming objects. These objects are then also merged with similar objects until a user-defined, unitless scale is reached. The similarity of the objects is also user-defined and is a trade-off between spectral and spatial homogeneity (Benz and others 2004). For this project, two scales were used. The first (scale = 15) broke the images into larger segments, while the second (scale = 8) used the objects from this first segmentation and divided them further. This second level was fine enough to isolate individual dead trees from the surrounding canopy (*fig. 4*).

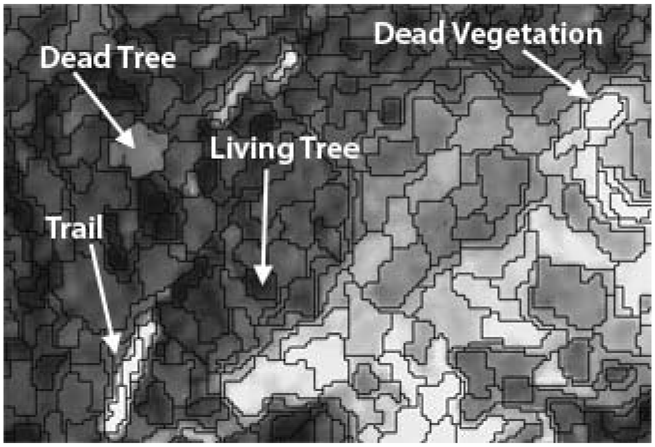

Figure 4—Image segments created by eCognition at scale = 8. Note the slightly lighter color of the dead tree in the middle of the image and its contrast with the bright white of the trail in the lower left.

Classification of the Imagery

The larger scale (scale = 15, Level 15, *fig. 5*) was used to mask non-vegetation objects from areas of vegetation. Non-vegetation objects most often consisted of urban land cover (houses, roads, etc.) but also included areas of bare soil and hiking trails. At the smaller scale (scale = 8, Level 8, *fig. 5*), the objects from Level 15 were broken into more detailed classes. These classes included Trees, Dead Trees, Not Vegetation, Other Vegetation, and Shadows, although Shadows and Other Vegetation were merged for the purposes of gap analysis. Data from Liu and others (2006b) was brought in as a thematic layer to enhance classification by reducing misclassification of deciduous trees as dead trees. The Dead Trees class consisted of standing dead trees; trees with catastrophic failures or snapped stems were classified as Other Vegetation. In this study, overstory mortality is assumed to be caused by *P. ramorum* based on the findings of Swiecki and Bernhardt (2002). Classification accuracy was determined by 250 random points scattered randomly across all classes, and the status of those points was visually assessed from the digital imagery. A two-meter buffer was included around these points to account for up to two pixels of variation in the segmentation process. Overall accuracy was 94.8 percent.

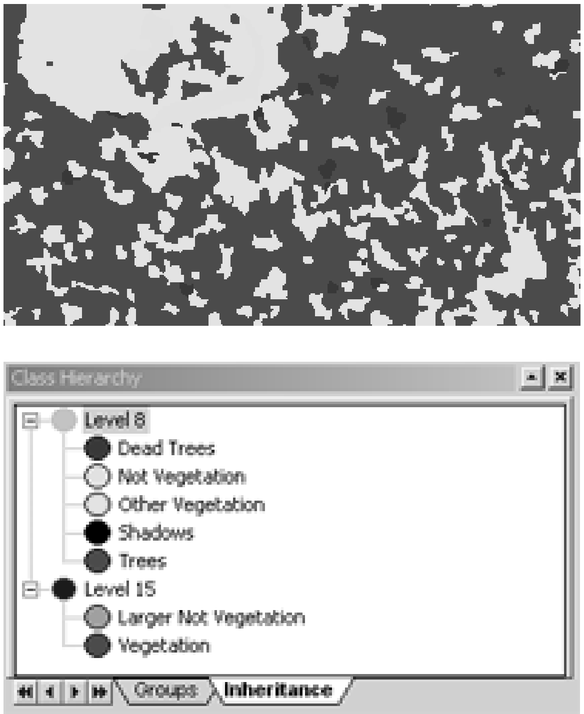

Figure 4—Sample of the classified image from 2000 (top) and the class hierarchy for eCognition (bottom). The class hierarchy defines the features and their fuzzy memberships for the classification. The levels mask user-selected classes defined at the larger scale (Level 15 in this case) from interfering with classification at smaller scales (Level 8).

Spatial Analysis and Processing of Gap Data

Non-tree gaps were merged into continuous objects and exported from eCognition as raster data. Once exported, Fragstats (McGarigal and others 2002) was used to determine each gap's area, perimeter, perimeter-to-area ratio (PA ratio) and Euclidean nearest neighbor (ENN). The raster output from Fragstats for each year was then converted to a shapefile and imported into a PostGIS database (Refractions Research 2005), an open-source spatially-aware relational database. In PostGIS, the gaps were overlaid with polygons of the Dead Tree class. Those gap polygons that contained dead trees and other non-tree vegetation were transferred to a new table for further processing. Using a custom Perl script, canopy gaps in 2001 were compared to canopy gaps containing dead trees in 2000. Those that spatially overlapped were associated and uniquely identified. The output of this script was then used to pair each individual gap to its Fragstats data.

Gaps over 3 ha were discarded from further analysis as they were primarily caused by urbanization and SOD. Three hectares is still above what has been previously considered in the literature (e.g., Hubbell and others 1999, Yamamoto 1993), but this threshold was kept due to the fractal nature of many of the larger (> 0.2 ha) SOD containing gaps.

Results

The classified imagery returned a total of 910 gaps from the year 2000 that matched the following criteria: 1) contained one or more dead tree crowns, 2) overlapped with one or more gaps in the following year, and 3) was under 3 ha in size. To make analysis possible, multiple gaps from 2001 that overlapped with a single gap from 2000 had their areas and perimeters summed, PA ratios recalculated from these values, and minimum ENN selected. The resulting data for all measures of gap structure were significantly non-normal by the Wilks-Shapiro W test in JMP 5.1.2 (SAS Institute Inc. 2005). In fact, area, perimeter, and ENN all showed significant right skewness. As a result, parametric methods were discarded in favor of the Wilcoxon signed-rank test and Hodges-Lehmann estimators in R (R Development Core Team 2006), both of which are robust in the face of non-normality.

***Table 1**—Median changes in gap parameters from 2000 to 2001 and summary statistics for 2000 and 2001*

	Area (m^2)	Perimeter (m)	PA Ratio	ENN (m)
Median Change	-59	-19.5 2207.673	2207.673	2.716
95% C.I.	-65.5, -53.5	-22, -17	2080.7, 2335.5	2.349, 3.102
2000				
Median	104	58.0	5911.9	5.0
Range	43–27,861	28–6398	2043.9–9508.2	2.0–34.234
2001				
Median	57	42.0	7586	7.616
Range	8–17,890	12.0–4974	2095–16000	2.0–57.870

Between 2000 and 2001, gap area declined by a median of 59 m^2, and perimeter decreased by a median of 19 m. PA ratio increased by a median of 2207.67, and ENN increased by a median of 2.716 m (*table 1*). The area of the gaps ranged from 43 m^2 – 2.786 ha in 2000 and 8 m^2 – 1.789 ha in 2001. Their perimeters varied from 28 – 6,398 m in 2000 and 12 – 4,974 m in 2001. These ranges of values produced different perimeter-to-area ratios as well, from 2,043.9 – 9,508.2 in 2000 and 2,095 – 16,000 in 2001. ENN was similarly varied between the two years, from 2.0 – 34.234 m and from 2.0 – 57.870 m in 2000 and 2001 respectively. A total of 796 gaps had their areas decrease, while 716 had their perimeter decrease. By the Wilcoxon rank sums test, the areas that increased between 2000 and 2001 were smaller in size on average than those that decreased.

Discussion

This work examined the persistence of gaps from 2000 to 2001, and as such, it is preliminary. We plan on continuing these analyses for the four years for which we have imagery to develop a more complete understanding of trends in gap structure. The existence of 910 canopy gaps, containing one or more dead trees in 2000, and persisting from year-to-year is indicative of the impact SOD has had on the over 900 ha of forested area in the China Camp area. Given the large number of gaps under 3 ha in size, with many of them fractal in shape, this pathogen has created far more edge within the bounds of the forest than had previously existed. In the year 2000, those gaps containing SOD mortality represented about 4 percent of the China Camp open space, totaling 33.43 ha in size and bordering just over 123 km of forest edge. The Euclidean nearest neighbor distances (*table 1*) indicate that these gaps have affected portions of the forest quite heavily. In these areas, the short distances between nearest neighbor gaps have increased the area of the forest influenced by edge effects.

The ability to look at these landscape level changes is useful, but the real details lie in the changes seen in the individual gaps. The fact that smaller gaps are more likely to grow in size is particularly interesting, as it could be indicative of a number of things. First, these gaps may have had trees die between 2000 and 2001. SOD infections have exhibited spatial clumping (Kelly and Meentemeyer 2002), so trees that were dead in 2000 may have infected a foliar host, such as California bay, which in turn can serve as a reserve of inoculum and spread the pathogen to other coast live oaks. When those trees died in 2001, they increased the size of the gap. In the future, as these gaps become large enough, they may plateau and begin to shrink as did those larger gaps from 2000. The incursion of existing crowns or the recruitment of new trees may work to close these larger gaps faster than SOD can expand them. While intriguing, this hypothesis has yet to be fully tested. Whether these gaps are more rapidly filled by existing canopies, recruitment of coast live oak seedlings and saplings, or pioneer species is an unknown at this point, leaving the successional trajectory of these openings similarly vague.

The number of shrinking gaps is just one sign that the forest canopy is expanding into the openings created by SOD. The median decrease in area of 59 m^2 is roughly the size of one or two mature canopies. Another sign of canopy expansion can be seen in the Euclidean nearest neighbor distances. Median ENN grew 2.716 m between years, indicating either a more evenly spaced distribution of SOD-related gaps or an increase in core forest area. Given the clumped distribution of SOD, the latter is a more likely explanation and a further sign of the forest closing the gaps.

Conclusion

Sudden oak death is significantly impacting the canopy of China Camp's oak woodlands. We identified 910 gaps containing dead trees in 2000 that persisted as canopy gaps in 2001, a large number that has changed the canopy structure across the area. Of those gaps, however, the majority appear to be decreasing in both area and perimeter, likely as a result of the expansion of the crowns of neighboring trees. This majority also tends to be larger on average than those that are growing in size. These smaller gaps may be expanding as a consequence of the spread of the pathogen and its effect on neighboring trees.

This work is still in its infancy. Pending analysis of the imagery for 2002 and 2003 should describe changes to the canopy in the wake of *P. ramorum* in greater detail. Object-based image analysis and multi-temporal geographic information systems have shown great promise in tracking changes to the forest canopy. To more fully understand the after-effects of SOD on California's oak woodlands, however, we will need to expand our scope both spatially and temporally.

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Continue

Community Ecology

Continue

Diversity and Abundance Comparisons Between Vineyard and Grazing Land Adjacent to Oak Woodland[1]

Dan Meade,[2] LynneDee Althhouse,[2] and Royce Larsen[3]

Abstract

Animal and plant species diversity, abundance, and distribution were examined across a landscape that included areas transformed from annual grass rangeland to agricultural production. Surveys were conducted quarterly over four years within an area recently placed in agricultural use and in undisturbed grassland. Here, we report results from bird and insect components of the surveys. Vineyard habitat and annual grassland habitat were compared with respect to statistical differences in species number, and population number. A higher diversity and abundance of survey organisms was found within the vineyard than in annual grassland habitat. Compared to undisturbed grassland the vineyard areas provide a more complex habitat supporting more species and larger populations of insects and birds. The study raises questions regarding the effect of vineyards on adjacent habitats, the value of vineyard habitats to species other than crop plants, and whether management protocols can prevent development of wildlife sinks within vineyards and orchards.

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[2] Althouse and Meade, Inc. Biological and Environmental Services.

[3] UC Cooperative Extension. mailto: relarsen@ucdavis.edu.

Continue

Effects of Wild Pigs on Seedling Survival in California Oak Woodlands[1]

Rick A. Sweitzer[2] and Dirk H. Van Vuren[3]

Abstract

Wild pigs were established around coastal Spanish settlements in California in the 1800s and expanded over the last century by hunting introductions, domestic releases, and natural dispersal. The current distribution of wild pigs is closely associated with oak woodlands where foraging and rooting by the species may impinge on many native species. Rooting disturbance by wild pigs may be especially problematic for regeneration of oak woodlands by physical damage to tree seedlings. In 1998 we initiated a long-term study of the ecological effects of wild pigs in California oak woodlands using multiple exclosures paired with nearby control plots that were established in two state parks in the north and central coast region of California, Austin Creek State Recreation Area and Henry Coe State Park. Mesh size and height of exclosure fences were designed to repel wild pigs but allow access by other organisms. We were especially interested in rooting effects on oak seedling number and size. The focus period for the 8-year study ended in May 2005, during which we monitored seedlings in (1) large 50 X 50 m exclosure and control habitat plot pairs centered in oak woodland, and (2) smaller 3 X 3 m exclosure and control canopy plot pairs established beneath the canopies of individual trees producing large crops of acorns in fall 1998 and 1999. In May 2005 the differential for seedling number in exclosure compared to control plots exceeded 400 percent at Austin Creek SRA. An outbreak of tent caterpillars limited seedling production at Henry Coe SP prior to 2003. Nevertheless, mean seedling height was significantly taller for all exclosure plots at both research sites. Rooting was reduced at Henry Coe SP after a control program was initiated in 2002, indicating that such approaches can improve the prospects for regeneration of oak woodlands in California.

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 were first introduced to California during the Spanish colonization period of the late 1700s and early 1800s (Giusti 1993, Sweitzer 1998). By the mid 1800s, scattered populations of wild pigs were established around a number of coastal settlements and Spanish missions. After a 50- to 75-year period of relative stasis, the distribution of feral pigs expanded after the 1950s to encompass many inland areas associated with California's diverse and widespread oak woodland ecosystem. This recent expansion by wild pigs into 49 of California's 58 counties appears related to some combination of natural dispersal by a growing statewide population and continued introductions (Waithman and others 1999). Expanding wild pig populations in California and elsewhere (Mayer and Brisbin 1991) are widely

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[2] Associate Professor, Department of Biology, University of North Dakota, Grand Forks, ND 58202. e-mail: richard_sweitzer@und.nodak.edu.

[3] Professor, Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, CA 95616. e-mail: dhvanvuren@ucdavis.edu.

viewed as a major conservation problem because of ecological damage from their foraging activities, most notably rooting.

Rooting by wild pigs disturbs and overturns surface vegetation and associated belowground plant tissues, thereby exposing the underlying soils to drying, warming, and erosion. By reducing herbaceous cover, rooting may alter competitive relationships among plants to the detriment of disturbance intolerant native species (Spatz and Muller-Dombois 1975, Cushman and others 2004, Kotanen 2004). Rooting also has been shown to alter soil nutrient processes by the combined effects of aeration, mixing of different soil layers, and increased water infiltration that may leach some nutrients (Lacki and Lancia 1986, Cushman and others 2004). Moreover, rooting physically damages or breaks seedlings, thereby limiting tree seedling survival (Bruinderink and Hazebroek 1996, Ickes and others 2003, Sweitzer and Van Vuren 2002).

Previous studies of wild pigs in mainland California have provided information on the population ecology of wild pigs (Barrett 1978, Schauss and others 1990, Sweitzer and others 2000) and the effects of rooting on plant communities (Cushman and others 2004, Kotanen 2004). In 1998, we initiated a large-scale study of the ecological effects of wild pigs in oak woodland ecosystems. Research began in May 1998 and continued through July 2005. The primary objectives of the study were (1) to assess the effects of rooting and foraging by wild pigs on the diversity and abundance of native and nonnative plants and terrestrial vertebrates (small mammals, reptiles and amphibians), and (2) to determine whether wild pig activities limit tree regeneration, thereby threatening important components of California's oak woodland ecosystem. 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. In this paper, we focus on aspects of the study related to objective 2; an experimental investigation of the effects of wild pigs on oak tree regeneration.

Methods

Study Areas

As previously detailed by Sweitzer and Van Vuren (2002), research sites selected for this study were state park areas in the central and north coast regions of California where high-density wild pig populations were found (Sweitzer and others 2000) and free-ranging livestock were absent. Herein we will describe aspects of research conducted at Austin Creek State Recreation Area (Austin Creek SRA; 38°34'6"N, 123°2'7"W) from fall 1988 to summer 2005 and Henry Coe State Park (Henry Coe SP; 38°12'40" S, 121°30'51"W) from summer 1999 to summer 2005. Austin Creek SRA and Henry Coe SP were experimental research sites where we obtained permission to establish fenced exclosures of different sizes; 50 x 50 m habitat plot exclosures and 3 x 3 m oak canopy exclosures. Comparative research also was conducted at two other sites that were very near each other but varied in wild pig density; Sugarloaf Ridge SP (38°27'25"N, 122°31'21"W) and McCormick Sanctuary (38°28'46"N, 122°33'47"W) in Sonoma County. Wild pigs were maintained at very low density at Sugarloaf Ridge SP by long-term pig control, whereas wild pig density was higher at McCormick Sanctuary where there was no organized trapping or shooting of wild pigs. Research at Sugarloaf Ridge SP and McCormick Sanctuary ended in fall 2000, and data relevant to oak regeneration were described by Sweitzer and Van Vuren (2002) as summarized below.

Austin Creek SRA is a 2,430 ha park in western Sonoma County near Guerneville, California. Elevation at the site ranges from 46 m to 458 m over a varied topography of steep canyons, rolling hills, and flat valley bottoms. Woodland habitats include a diverse mix of Oregon oak (*Quercus garryana*), coast live oak (*Q. agrifolia*), black oak (*Q. kelloggi*), bay laurel (*Umbellularia californica*), Douglas fir (*Pseudotsuga menziesii* var *menziesii*), madrone (*Arbutus menziesii*), and coastal redwoods (*Sequoia sempervirens*) with an understory including *Festuca californica*, *Trifolium* sp., and *Cynosurus echinatus*. Grassland habitats are mostly dominated by annual grasses (*Briza maxima*, *Bromus hordeaceous*, *Avena* sp.), some perennial bunchgrasses (*Danthonia californica*), and a wide variety of forbs (*Geranium dissectum*, *Hypochaeris glabra*, *Lotus micranthus*, *Trifolium* sp.). Henry Coe State Park is a large 35,207 ha park located in Santa Clara County east of the cities of Morgan Hill and Gilroy, California. Elevation at the site ranges from 216 m to 1,085 m. Research was focused in the southwestern area of the park where the landscape is dominated by high ridges and deep canyons. Habitats range from open grasslands and open savannah woodlands to dense stands of chapparal/chamise (*Adenostoma fasciculatum*) brush. Grassland habitats include a mix of annual and perennial grasses and forbs (*Avena* sp., *Bromus* sp., *Nassella pulchra*, *Melica californica*, *Trifolium* sp., *Viola* sp.), whereas woodlands are dominated by blue oak (*Q. douglasii*) and gray pine (*Pinus sabiniana*) with occasional coast live oak, valley oak (*Q. lobata*), and bay laurel.

Wild Pigs and Oak Regeneration Potential

The combined effects of intensive foraging on acorns in the fall and widespread rooting during the October to late April wet season may reduce oak tree regeneration in California oak woodlands. Acorn consumption by wild pigs reduces the number of seeds that might otherwise germinate, whereas rooting physically damages or uproots young seedlings. We used four different approaches to assess this hypothesis: (1) comparisons of data on tree seedling sizes along multiple, randomly positioned 4 x 40 m "belt transects" in oak woodland and mixed forest habitats among comparative and experimental research sites varying in wild pig density; (2) monitoring numbers of naturally falling acorns on small plots nested within oak canopy exclosure and control plots beneath multiple high masting oak trees at experimental research sites; (3) comparison of numbers and sizes of tree seedlings in oak canopy exclosure and control plots at experimental research sites; and (4) comparisons of data on tree seedling size and number along belt transects in 50 x 50 m exclosure and control habitat plots in oak woodland and mixed forest areas at experimental research sites.

In a prior paper we reported fewer large oak tree seedlings (≥ 200 mm) along seedling belt transects in oak woodland habitats at research sites with high and very high density wild pigs (Austin Creek SRA and Henry Coe SP, respectively) compared to sites with moderate and very low density wild pigs (McCormick Sanctuary and Sugarloaf Ridge SP, respectively; Sweitzer and Van Vuren 2002). We further described evidence for reduced survival for acorns in control compared to fenced oak canopy plots at Austin Creek SRA and Henry Coe SP (Sweitzer and Van Vuren 2002). To facilitate a more thorough examination of the effects of wild pigs on tree regeneration, we continued monitoring the number and sizes of tree seedlings in habitat and oak canopy control and exclosure plots at Austin Creek SRA and Henry Coe SP from spring 2000 to summer 2005.

Habitat Plot Experiments

Several research activities were focused around 50 X 50 m habitat plot exclosure and nearby control plots in grassland, oak woodland, mixed forest, and meadow habitats. At Austin Creek SRA, we established one 50 x 50 m fence exclosure in each of the four habitat types in summer 1998. Research was initiated at Henry Coe SP in summer 1999 when two 50 x 50 m habitat exclosures each were established in grassland and oak woodland habitats. Fences were designed to allow foraging access by all herbivores except wild pigs, and were constructed in the field by wiring 0.9 m woven wire 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 staked out a matched 50 x 50 m control plot usually within 500 m of the exclosure. Nested within each 50 x 50 m habitat exclosure and control plot were (1) a 7 x 7 small mammal live trap grid with 8 m spacing between lines, (2) six 4 x 40 m seedling belt transects between and parallel to trap grid lines, (3) a y-shaped pitfall trap array with ten 7.6 liter bucket traps buried to ground level, and (4) several 2 x 2 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.

Beginning in May 2000 and every year thereafter until May 2005, we enumerated and measured tree seedlings along each of the six belt transects at all *woodland habitat exclosure and control plots* at Austin Creek SRA and Henry Coe SP; tree seedlings were not present in grassland or meadow habitats.

All seedlings of trees or woody shrubs ≤ 1.5 m (1500 mm) were measured (±2 mm) and identified when possible. We also measured seedlings that originated from the base of dead and living trees, recording these as basal sprouts. Data on tree seedlings along belt transects in woodland habitat exclosure and control plots for Austin Creek SRA and Henry Coe SP were analyzed separately because exclosures were set up one year earlier at Austin Creek SRA. An analysis of variance (ANOVA) model (Zar 1999) was used to compare mean oak seedling size between exclosure and control habitat plots at the end of the monitoring period in spring 2005.

We estimated soil disturbances from wild pigs, rodents (*Thomomys* sp.), and research activities in all oak woodland habitat exclosure and control plots during the study by line-intercept sampling. Six, parallel 50 m line transects were extended across each plot, whereupon we measured the intercept distances (± 1 cm) of all areas of bare soil along each transect.

Oak Canopy Exclosure Experiments

Oak canopy exclosure experiments were originally established beneath the canopies of high masting oak trees in summer 1998 (Austin Creek SRA) and summer 1999 (Austin Creek SRA, Henry Coe SP) to assess the extent to which acorn foraging by wild pigs reduced resource availability for native wildlife. As further detailed by Sweitzer and Van Vuren (2002), multiple high mast producing oak trees were identified at each research site in summers 1998 and 1999, whereupon the corners of two 3 x 3 m plots were delineated beneath appropriately matched areas of the canopies of the trees. Exclosure and control designations were then randomly assigned, whereupon fences were built around the exclosure plots using the same design features as habitat plot exclosures. Research to estimate and compare acorn survival between fenced and non-fenced canopy plots was completed in December 1999, but most of the plots were left in place for assessing tree seedling number and size.

At Austin Creek SRA canopy plot experiments were established beneath a total 16 *Q. kellogi*, two *Lithocarpus densiflorus*, five *Q. agrifolia*, two *Q. lobata*, and one *Q. garryana* in 1998 and 1999 combined. Six canopy plot experiments were removed in summer 1999 prior to establishing canopy plots at ten newly identified high masting oak trees. Among all of these trees, canopy plot exclosures were retained and seedlings monitored at ten *Q. kellogi*, two *L. densiflorus*, five *Q. agrifolia*, and one *Q. garryana* from 2000 to 2005. One additional *Q. kellogi* was monitored from 2000 to 2004 until a large portion of the tree fell over the control canopy plot in 2004. At Henry Coe SP, canopy plot experiments were established beneath six *Q. douglasii*, three *Q. agrifolia*, and six *Q. lobata*. All canopy plots were retained and monitored for seedling number and size from 2000 to 2005.

Data on oak tree seedlings among canopy plots at Austin Creek SRA and Henry Coe SP were analyzed separately because exclosures were established one year earlier at Austin Creek SRA, and the species of individual oaks used for canopy plot experiments varied between sites. Data on the mean number and size of oak seedlings at the end of the monitoring period were evaluated by ANOVA.

In each year of the study, we estimated the area of each canopy control plot that was disturbed by rooting from scaled-down line drawings (Sweitzer and Van Vuren 2002). Line drawings of rooted areas were prepared for each 3 x 3 m canopy control plot around mid May of each year prior to enumerating and measuring individual tree seedlings. Line drawings were subsequently analyzed using a grid overlay technique to estimate the proportion of each canopy control plot disturbed by rooting.

All means are reported ± 1 standard error (SE).

Results

Habitat Plot Seedlings

At Austin Creek SRA, there were four times as many oak tree seedlings along six belt transects within the oak woodland habitat plot exclosure (*n*=2201) compared to along six belt transects in the oak woodland habitat control plot (*n*=550) after seven years of protection from wild pigs (*fig. 1a*). Height of tree seedlings in the oak woodland habitat exclosure plot averaged 83.0 ± 0.88 mm, compared to 74.0 ± 1.8 mm in the oak woodland habitat control plot ($\alpha < 0.001$; *fig. 2a*). In mixed woodland habitat plots at Austin Creek SRA, there were 95 total oak seedlings (mean seedling height 84.4 ± 3.3 mm) along belt transects in the exclosure plot, compared to only eight oak seedlings (mean seedling height 167.9 ± 43.3 mm) along belt transects in the control plot. At Henry Coe SP, there were more total oak seedlings (*n*=852) along belt transects in exclosure habitat plots compared to control habitat plots (*n*=742) after six years of protection from rooting. Oak tree seedlings in the exclosure habitat plots were taller (mean = 85.3 ± 1.2) than those in the control habitat plots (mean = 69.3 ± 1.2; $\alpha < 0.001$).

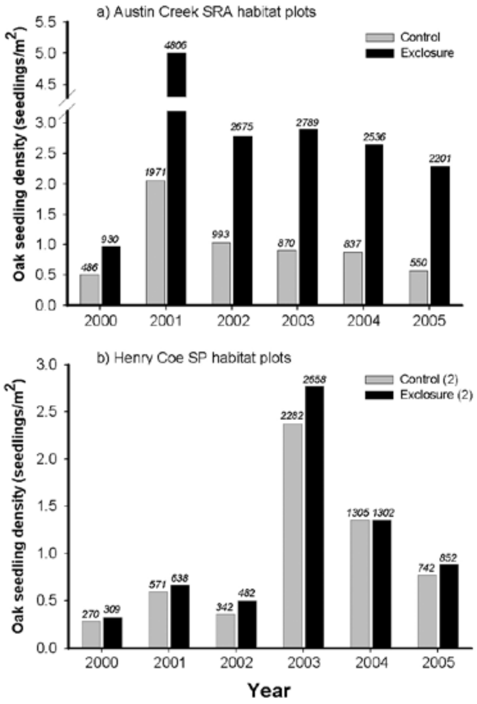


Figure 1—Variation in total number (above bars) and density of oak tree seedlings for the total area searched along six (Austin Creek SRA) or twelve (Henry Coe SP) 4 x 40 m belt transects in oak woodland habitat exclosure and control plots at (a) Austin Creek SRA and (b) Henry Coe SP from spring 2000 to spring 2005.

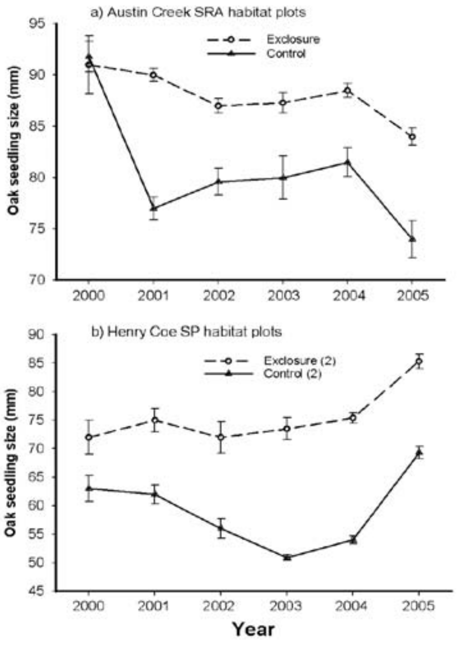


Figure 2—Variation in mean height (± SE) of oak tree seedlings along 4 x 40 m belt transects in oak woodland habitat exclosure and control plots at (a) Austin Creek SRA and (b) Henry Coe SP from spring 2000 to spring 2005.

Oak woodland control habitat plots at both Austin Creek SRA and Henry Coe SP experienced higher levels of soil disturbances than exclosure habitat plots over the six-year seedling monitoring period (*fig. 3*). Soil disturbances were predominantly from rooting by wild pigs; other sources of bare soil were rodent diggings and researcher activities (pitfall arrays, trails, etc.).

At Austin Creek SRA, there were over five times as many oak tree seedlings in the exclosure canopy plots compared to the control canopy plots at the end of the monitoring period (*fig. 4a*). Oak tree seedlings in the exclosure canopy plots were taller (mean = 123.1 ± 3.2) than those in the control canopy plots (mean = 85.1 ± 6.6; $\alpha < 0.001$; *fig. 5a*). Monitoring results from Henry Coe SP identified around two times as many oak tree seedlings in exclosure compared to control canopy plots (*fig. 4b*). Similar to data from Austin Creek SRA, oak tree seedlings in the exclosure canopy plots were taller (mean = 113.0 ± 2.2mm) than those in the control habitat plots (mean = 80.8 ± 1.8; $\alpha < 0.001$; *fig. 5b*).

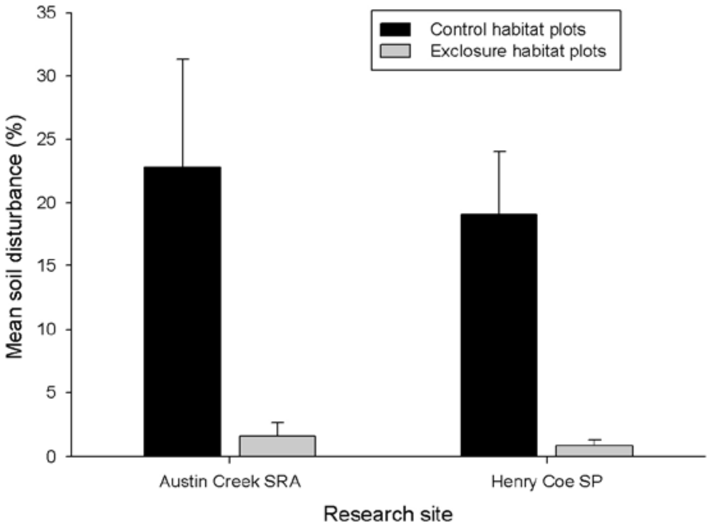
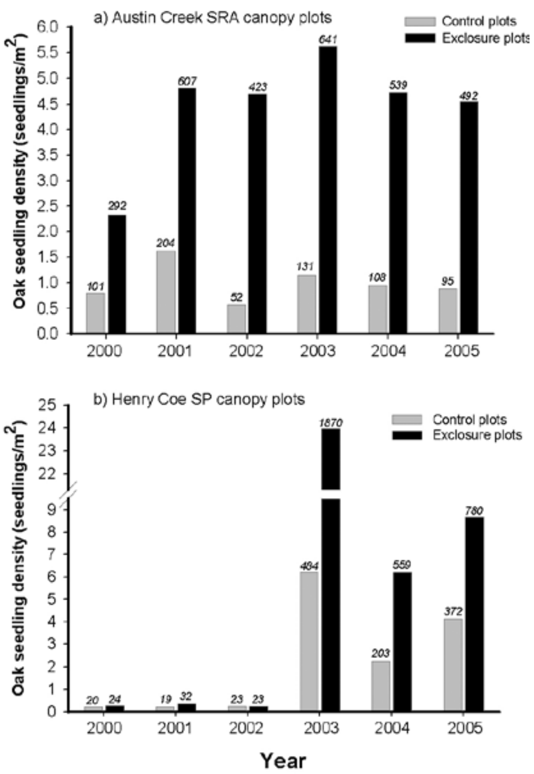


Figure 3—Differences in the estimated mean soil disturbances based on line-intercept sample transects in oak woodland control and exclosure habitat plots at Austin Creek SRA and Henry Coe SP over the tree seedling monitoring period (spring 2000 to spring 2005). Means are with 1 SE.

Over the six-year monitoring period, wild pig rooting disturbance in oak canopy control plots averaged 45.5 percent (± 6.4 percent) for the 18 trees being monitored at Austin Creek SRA, and 22.0 percent (± 6.2 percent) for the 15 trees being monitored at Henry Coe SP.



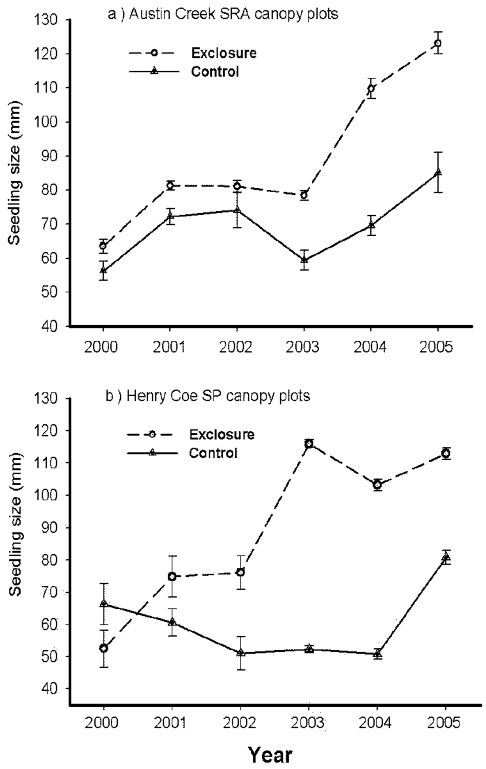


Figure 4—Variation in total number (above bars) and density of oak tree seedlings for the total area searched among multiple 3 x 3 m canopy exclosure and control plots at (a) Austin Creek SRA and (b) Henry Coe SP from spring 2000 to spring 2005.

Figure 5—Variation in mean height (± SE) of oak tree seedlings in 3 x 3 m canopy exclosure and control plots at (a) Austin Creek SRA and (b) Henry Coe SP from spring 2000 to spring 2005.

Discussion

We observed and documented a strong and consistent wild pig-related reduction in the number and size of oak tree seedlings in oak woodland habitats at two widely separated research sites in California. With the exception of oak woodland habitat plots at Henry Coe SP, the final differential for numbers of oak seedlings in fenced plots was at least double the number of seedlings in the control plots (*figs. 1, 4)*. The reduction in seedling number in the control plots could be directly attributed to wild pigs, because the plot areas experienced variable but significant levels of rooting over the six-year monitoring period (*fig. 3)*.

One notable difference between the Austin Creek SRA and Henry Coe SP research sites was the relatively low number of oak seedlings for habitat and canopy plots at Henry Coe SP in the first several years of the study. In research years 2000 and 2001, we observed a major population outbreak of tent caterpillars (*Malacosoma californicum*) at Henry Coe SP. The tent caterpillar outbreak at Henry Coe SP was very severe in spring 2000, and resulted in most oak trees being almost completely defoliated in June 2000. By early fall 2000, many oaks at Henry Coe SP had produced a second set of leaves, likely a major nutrient cost to their systems. Although we also observed some tent caterpillars at the Austin Creek SRA site in spring 2000, the insects were nowhere near as abundant as at Henry Coe SP and widespread defoliation did not occur at Austin Creek SRA. The tent caterpillar outbreak at Henry Coe SP had subsided by fall 2001, potentially contributing to oak trees at the site producing a major seed crop in fall 2002 (*figs. 1, 4).* Although we did not directly monitor acorn mast production at either research site during the study, acorn production at Austin Creek SRA appeared more regular than at Henry Coe SP, potentially explaining the overall higher numbers of oak seedlings at Austin Creek SRA.

Although the final number of oak seedlings along belt transects in the mixed forest habitat exclosure (n = 95) far exceeded the number of oak seedlings in the mixed forest habitat control plot (n = 8), mean seedling size was taller in the control plot. Among the eight total seedlings in the habitat control plot were three that exceeded 200 mm, which inflated the mean for the plot that was already based on a small sample size.

Management Implications

Results from the first several years of this study were valuable for demonstrating reduced acorn survival in control areas compared to fenced plots (Sweitzer and Van Vuren 2002). Longer-term monitoring data for research through 2005 leave little doubt that rooting activities of wild pigs also reduces the number and size of oak tree seedlings in California oak woodlands. Research from other areas of North America and worldwide indicate that lethal control may help reduce ecological damage caused by feral pigs (Choquenot and others 1999, Engeman and others 2004).

We detected evidence for a reduction in rooting disturbance in our habitat control plots after managers at Henry Coe SP implemented a wild pig control program in winter 2002. During the first year and a half of the control program, wild pig trapping/shooting was focused in areas away from our research plots. After summer 2003, however, control efforts expanded to the southwestern area of the park, encompassing all of the habitat control and exclosure plots. Diminished rooting in many areas of the state park was readily evident after 2003. In our habitat control plots in grassland and woodland areas in particular, however, the estimated mean rooting was reduced from 19.1 ± 3.6 percent during the four-year research period prior to wild pig control (2000 to 2003) to a mean of 8.8 ± 3.0 percent in the two years after wild pig control ($\alpha = 0.07$). This wild pig control-related reduction in rooting disturbance likely contributed to the trend for increasing numbers of seedlings observed in our canopy and habitat plot control areas at Henry Coe SP that began in 2003 (*figs. 1, 3*).

In recent years, many state and national parks in California have initiated programs to control wild pigs to protect natural resources. These results are important for suggesting that lethal control efforts directed at wild pigs can improve the prospects for oak seedling survival in California oak woodlands.

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Continue

Nest-Site Habitat of Cavity-Nesting Birds at the San Joaquin Experimental Range[1]

Kathryn L. Purcell[2] and Jared Verner[2]

Abstract

Detailed information about the nesting habitats of birds, including those needed for successful nesting, can provide a better understanding of the ecological factors that permit coexistence of different species and may aid in conservation efforts. From 1989 through 1994, we studied the nesting habitat of secondary cavity-nesting birds in oak woodlands at the San Joaquin Experimental Range, Madera County, CA. We measured habitat surrounding nests and examined similarities and differences in nesting habitat used by eight species to evaluate overlap in nesting habitat use and possible competition. Nesting habitat of Bewick's Wrens (*Thryomanes bewicki*i) was unique among the species studied. Their nests were the lowest and located in the densest habitat on the steepest slopes where interior live oaks (*Quercus wislizenii*) were abundant. Nesting habitat was similar among European Starlings (*Sturnus vulgaris*), Western Bluebirds (*Sialia mexicana*), and Violet-green Swallows (*Tachycineta bicolor*). These species all nested in open areas with the highest density of blue oaks (*Quercus douglasii*), the lowest densities of live oaks and snags, and the lowest basal area of trees. Nests of White-breasted Nuthatches (*Sitta carolinensis*) were similar to the above three species, differing only in being lower compared to nests of European Starlings. Ash-throated Flycatcher (*Myiarchus cinerascens*) nesting habitat was characterized by dense stands of trees with a high density of live oaks and snags. Oak Titmouse (*Baeolophus inornatus*) nests were low and located in high-density stands of live oaks on steep slopes. House Wrens (*Troglodytes aedon*) nested in dense stands of trees. Successful Ash-throated Flycatcher and Oak Titmouse nests had higher basal area of live trees compared to unsuccessful nests and, compared to other species, habitat surrounding their nests had high basal area. European Starling nests were highest, and nests located high in trees had higher nest survival. Consequently, these three species tended to select nest sites in habitats where they had higher nest success. We recommend management activities that maintain habitat diversity, including areas that differ in tree species composition and density, to promote species diversity.

Keywords: Competition, European Starling, nest success, nest-site habitat, oak woodlands, secondary cavity-nesting birds, Sturnus vulgaris.

Introduction

Habitat features can influence nest-site quality and reproductive success (Martin and Roper 1988). Because nest-site selection in birds is closely tied to fitness, habitat features of nest sites that influence productivity should be under strong selection pressure. Habitat features that influence productivity can also influence the coexistence of species, as well as nest-site quality and reproductive success (Martin and Roper 1988). Species that overlap in nest-site selection criteria, for example, have been shown to experience higher predation rates, and such costs can favor use of nests sites that differ (Martin 1988, 1996). Processes such as competition and predation determine how many and which species coexist. Therefore, differences in

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[2] Research Wildlife Biologist, and Research Wildlife Biologist, retired, respectively, Forestry Sciences Laboratory, Sierra Nevada Research Center, Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, 2081 E. Sierra Ave., Fresno, CA 93710.

nest sites among species may reflect selection for coexistence of species with nest sites that differ (Martin 1988, 1996). Understanding the nesting habitat requirements of coexisting species should provide a better understanding of the ecological factors related to the abundance and distribution of species and the ability of species to coexist.

Competition for limited nest sites may force use of suboptimal sites (Li and Martin 1991). Cavities are often limiting for cavity-nesting species (Brush 1983, Stauffer and Best 1982), although this is not always the case. When European Starlings (*Sturnus vulgaris*), a non-native species known to compete for nest sites with native cavity-nesting species, invade new habitats, their presence can contribute to nest-site limitation (see Wiens 1989, for review). Koenig (2003) found little evidence that the invasion of European Starling in North America has severely affected numbers of native cavity-nesting birds (Koenig 2003), although he recommended additional studies at the population level to confirm these results.

Nest-site selection can be thought of as operating on two spatial scales: the nest site, characteristics within the immediate vicinity of the nest, and the nest patch, characteristics of the habitat surrounding the nest (Martin and Roper 1988). Munro and Rounds (1985) found that nest box properties were more important than habitat variables in differentiating habitat use among species, but Holt and Martin (1997) found that vegetation structure surrounding the nest was important in determining occupation when nest sites were less limiting. Nest-site selection in Hermit Thrushes (*Catharus guttatus*) appeared to be a function of both nest site and nest patch characteristics (Martin and Roper 1988). Selected sites had a large number of potential nest sites in the surrounding area that predators would have to search to find a nest, thereby reducing predation risk.

If nest-site preferences are adaptive, nests located in preferred sites should be more successful. Use does not necessarily reflect preference, and nest-site selection may not be adaptive if nest sites are not equally available to all individuals. Competition for nest sites may result in niche shifts to minimize overlap with other species that lead to use of less than optimal conditions. Examination of associations between selected and successful nest sites can shed light on how processes such as competition and predation affect species' viability and coexistence.

In this study, we examined similarities and differences in nesting habitat of eight species of secondary cavity-nesting birds, including the European Starling. For three species, we examined differences between successful and failed nests to examine whether nest sites used were those in which individuals were most successful.

Methods

Study Area

The San Joaquin Experimental Range (hereafter SJER) is located in the western foothills of the Sierra Nevada, in Madera County, CA. It has an area of approximately 1,875 ha and ranges in elevation from 215 to 520 m. The climate is characterized by cool, wet winters and hot, dry summers. Annual precipitation averages 48.6 cm, with most falling as rain between November and March.

Habitat at SJER is classified primarily as blue oak-foothill pine (Mayer and Laudenslayer 1988). The sparse overstory is dominated by three tree species: blue oak (*Quercus douglasii*), interior live oak (*Q. wislizenii*), and foothill pine (*Pinus* *sabiniana*), but buckeye (*Aesculus californica*) and desert elderberry (*Sambucus mexicana*) also occur. Shrubs grow as scattered individuals or in denser clumps, and include wedgeleaf ceanothus (*Ceanothus cuneatus*), chaparral whitethorn (*C. leucodermis*), Mariposa manzanita (*Arctostaphylos viscida mariposa*), holly-leaf redberry (*Rhamnus ilicifolia*), and coffeeberry (*R. tomentella cuspidata*). In areas without shrubs, annual grasses and forbs dominate the understory. In some areas, the habitat is classified as blue oak woodland (Mayer and Laudenslayer 1988) where the overstory is primarily blue oak with a fairly open understory. SJER has been lightly to moderately grazed by cattle for approximately 100 years. A 29-ha research natural area has been ungrazed since 1934.

Fieldwork

We located and monitored nests of all species from 1989 to 1994. Two 30-ha plots, matched for total canopy cover, were searched most intensively. One of the plots was in grazed pastures and the other was in the research natural area. In 1992 to 1994, other areas within SJER were searched in addition to the two study plots to increase sample sizes and the range of habitats studied.

In 1989 to 1991, nests were checked every four to seven days using an automotive inspection mirror and a small light bulb. Nests were checked by using an extension ladder. Nests that could not be accessed with the extension ladder were observed from the ground. In 1992 to 1994, nests were checked every four to five days. We climbed to nests using various climbing techniques except when nests were in unstable substrates. Contents of nest cavities were observed with a fiberscope (Purcell 1997).

Nest age, or the number of days a nest was active at a given visit, was determined by extrapolating from identified events, such as the beginning of incubation, hatching, or fledging, and the appearance of nestlings. We were not able to determine the age of some nests, which were excluded from analyses of nest survival.

We examined habitat variables that we predicted would vary among species based on previous studies. Nest height has commonly been shown to differ across species and to influence nest predation rates in some species (Burhans and others 2002, Hatchwell and others 1999, Hooge and others 1999, Li and Martin 1991, Nilsson 1984). Because European Starlings are known to nest in open, relatively flat habitat dominated by blue oaks (Purcell and others 2002), we predicted that nesting habitat would vary among species in tree density, slope, and relative abundance of tree species and snags. Accordingly, the habitat variables we analyzed included nest height, basal area of live trees, numbers of blue oaks, live oaks, and snags surrounding the nest, and percent slope. For each active nest, nest height was measured using a clinometer and tape measure. Field crews recorded the number and species of trees and snags in a 0.04-ha plot (11.3 m radius) centered on the nest. This is a long- and widely-established plot size that allows comparisons among studies (James and Shugart 1970, Martin and others 1997). Basal area of live trees was measured with a basal area prism, and the slope of the nest plot was measured using a clinometer.

Statistical Analysis

We analyzed differences and similarities of nest habitats used by the nonexcavator species with MANOVA and Scheffe's multiple comparison procedure, controlling for Type I error rates (SAS Institute, Inc. 2004). Variables were examined for nonlinearity with generalized additive models using cubic spline smoothing (GAM; R Development Core Team 2003). Transformations suggested by GAM to describe the functional shapes of variables were obtained by trying logarithmic, quadratic, and square root functions. Results suggested the use of linear forms for nest height, number of snags surrounding the nest, and percent slope; logarithmic forms were suggested for basal area of live trees, number of blue oaks, and number of live oaks surrounding the nest.

We compared successful and failed nests for three species of secondary cavity nesters with sample sizes > 40 to examine whether the nesting habitat used by a species differed from the habitat where they were most successful. We used the logistic exposure method (Shaffer 2004) to investigate the importance of nesting-habitat variables to nest survival. This method allows evaluation of a broad array of covariates, evaluation of competing models, and does not require the assumption of constant daily survival rates or any assumptions about when nest failure occurs within an interval. Analysis is based on generalized linear models, assuming a binomial distribution and a logit link function. Analyses were done using Proc GENMOD (SAS Institute, Inc. 2004). Each visitation interval is treated as an observation.

Nest survival may change in relation to time-specific variables such as nest initiation date and stage of development. To control for potentially confounding effects of time-specific factors, we first considered linear, quadratic, and cubic effects of nest age; linear and quadratic effects of date; and a categorical effect of year, following Grant and others (2005). We evaluated 24 models that included a constant daily survival model (null model) and all combinations of age, date, and year effects. The most-supported time-specific model was included in subsequent analyses to control for potentially confounding effects of age, date, and year as the base model.

We examined 22 models containing all one- and two-variable combinations of the six variables included in the MANOVA and the base model. Models were ranked and compared using ΔAICc and Akaike weights (Burnham and Anderson 2002). Models with lower AICc scores are considered closer to the true model. Because ΔAICc is the difference between the best fitting model and model "i," models with low ΔAICc values have more support. Akaike weights can be interpreted as the probability that model "i" is the best model for the data at hand, given the set of models considered. Effective sample size, based on the total number of days that each nest was known to survive plus one day for each interval that ended in failure (Rotella and others 2004), was used to calculate AICc. We used model averaging to address model selection uncertainty. Variance estimates based on weighted averages of parameter estimates across all models reflect both uncertainty in parameter estimates and uncertainty in selecting that model. The relative importance of each variable was assessed by summing the Akaike weights over all models in which that variable appeared. This was possible because each variable occurred in the same number of models (6). Model fit of the global model was assessed with the Hosmer-Lemeshow decile of risks test (Hosmer and Lemeshow 2000). In all cases, the global model fit the data well (Ash-throated Flycatcher: $\hat{C} = 3.51$, $P = 0.89$, Oak Titmouse: $\hat{C} = 2.49$, $P = 0.96$, European Starling: $\hat{C} = 5.91$, $P = 0.66$).

Results

Nesting habitat differed across the eight nonexcavator species (*table 1*). Bewick's Wrens differed most from the other species and had extreme values for five of the six variables. Their nests were the lowest and were located in the densest habitat on the steepest slopes, where live oaks were abundant and blue oaks were sparse.

Table 1—*Means (sd) and results of MANOVA and Scheffe's multiple-comparison procedure to examine differences in nest habitat of nonexcavators. Wilks' lambda = 0.5395, df = 42, 1560.7, P < 0.0001. For each variable, species with the same letter did not differ.*

Species	*N*	Nest height (m)	Basal area of live trees (m^2/ha)	Number of blue oaks[1]	Number of live oaks[1]	Number of snags[1]	Slope (percent)
Ash-throated Flycatcher	43	3.8 (1.7) ab	10.9 (6.5) b	1.1 (1.6) a	7.6 (7.5) b	2.0 (2.5) b	12.7 (6.7) ab
Violet-green Swallow	24	4.9 (2.0) bc	6.3 (3.4) ab	2.4 (1.7) b	1.0 (2.3) a	0.1 (0.6) a	14.6 (6.7) b
Oak Titmouse	80	3.8 (1.9) b	11.2 (7.6) b	1.4 (1.8) ab	6.6 (8.1) b	1.3 (2.1) ab	13.8 (5.9) b
White-breasted Nuthatch	35	4.3 (1.7) b	9.5 (5.8) ab	1.6 (2.0) ab	3.9 (5.9) ab	0.7 (1.2) ab	11.9 (6.2) ab
Bewick's Wren	17	1.3 (1.7) a	13.8 (12.2) b	0.4 (1.2) a	7.9 (7.1) ab	1.3 (1.8) ab	16.4 (8.6) b
House Wren	40	4.5 (1.9) b	10.3 (6.7) b	1.5 (2.9) ab	4.6 (1.5) ab	1.5 (2.2) ab	12.2 (5.7) ab
Western Bluebird	31	4.0 (1.5) ab	5.6 (3.5) a	1.6 (1.5) ab	1.4 (3.1) a	0.3 (0.8) a	13.1 (6.1) ab
European Starling	85	7.4 (4.9) c	6.7 (5.7) a	1.8 (2.5) b	2.0 (4.9) a	0.4 (1.2) a	9.8 (4.3) a

[1] The number of blue oaks (*Quercus douglasii*), interior live oaks (*Q. wislizenii*) and snags in a 0.04 ha circular plot surrounding the nest tree.

Nesting habitats of starlings, bluebirds, and swallows were similar. All three species nested in open areas with low basal area of live trees, where blue oaks were abundant, and live oaks and snags were sparse. Starling nests were the highest and were found in the most level areas. Swallow nests were second in height after starling nests and were found on steeper slopes compared to starlings. Bluebird nests were intermediate in height, significantly lower than starling nests, and occurred in areas with the lowest tree density.

White-breasted nuthatch nests were intermediate in most respects and were similar to the above three species. They differed only in nest height from starling nests.

Ash-throated Flycatcher nesting habitat was characterized by dense stands of trees that included predominantly live oaks, and the greatest number of snags.

Oak Titmice nested lower than all other species except Bewick's Wrens, although only significantly lower than starlings, and their nests were located in dense stands with abundant live oaks on fairly steep slopes.

House Wren nests were intermediate in nest-habitat characteristics. Their nests tended to be fairly high and they were found in denser stands of trees.

Nest Survival

Sample sizes for examining correlates of nest success were adequate for three species: Ash-throated Flycatcher, Oak Titmouse, and European Starling. Nest survival was not constant over the nest period for any of the three species. The most-supported time-specific model for Ash-throated Flycatchers included a cubic effect of nest age. For Oak Titmice, the best model included a linear effect of nest age and a quadratic effect of nest date. Nest survival of European Starlings was best explained by a model that included quadratic effects of nest age.

Nesting habitat variables did not appear to be strong predictors of nest survival for Ash-throated Flycatchers (*tables 2 and 3*). The base model was the most-supported model and age of the nest was an important predictor of nest survival. Basal area of live trees had the highest relative importance value (*table 3*), suggesting that successful Ash-throated Flycatcher nests had higher basal area of live trees.

Variation in nest survival of Oak Titmice nests was best explained by basal area of live trees. The model containing only basal area received the most support, basal area was included in six of the seven top models (*table 2*), and it had a relatively high importance value (*table 3*). Successful Oak Titmice nests had higher basal area of live trees.

European Starling nests located high in trees had higher nest survival. Nest height alone was the most-supported model, it was included in the top six models (*table 2*), and it had a high importance value in relation to the other variables (*table 3*).

Table 2—*Model selection results for logistic-exposure models of daily survival rates for Ash-throated Flycatcher, Oak Titmouse, and European Starling nests. Twenty-two candidate models were considered that included all one- and two-variable combinations of nest height (Nest ht), basal area of live trees (Basal area), the number of blue oaks (Blue oak), interior live oaks (Live oak), and snags (Snag) in a 0.04-ha circular plot surrounding the nest tree, and slope (Slope). $Log_e(L)$ is the value of the maximized log-likelihood function, K is the number of parameters in the model, AIC_c is Akaike's information criterion corrected for small samples, ΔAIC_c is the difference between the best fitting model and model i , and* $\mathbf{w_i}$ *is the Akaike weight and indicates the relative likelihood that a model is the best model of those considered. All models included the best time-specific model (Base) for each species. Only models with $\Delta AIC_c \leq 2.0$ and the base model are shown. The effective sample sizes are as follows: Ash-throated Flycatcher - 828 exposure days, based on 44 nests; Oak Titmouse – 2,557 exposure days, based on 99 nests; European Starling – 1,895 exposure days, based on 76 nests.*

Model	**K**	**$Log_e(L)$**	**AIC_c**	**ΔAIC_c**	**w_i**
		Ash-throated Flycatcher			
Base[1]	4	-47.0	102.0	0.0	0.13
Basal area	5	-46.1	102.3	0.3	0.11
Live oak	5	-46.5	103.1	1.1	0.07
Snag	5	-46.6	103.3	1.3	0.07
Basal area + Slope	6	-45.8	103.6	1.6	0.06
Slope	5	-46.9	103.9	1.9	0.05
Basal area + Blue oak	6	-45.9	104.0	2.0	0.04
		Oak Titmouse			
Basal area	5	-88.8	187.6	0.0	0.14
Base[2]	4	-90.0	188.1	0.47	0.11
Basal area + Blue oak	6	-88.4	188.9	1.28	0.08
Basal area + Slope	6	-88.5	189.0	1.39	0.07
Basal area + Live oak	6	-88.6	189.2	1.62	0.06
Nest ht + Basal area	6	-88.7	189.4	1.78	0.06
Basal area + Snag	6	-88.7	189.4	1.81	0.06
		European Starling			
Nest ht	4	-65.3	138.6	0.0	0.24
Nest ht + Live oak	5	-64.9	139.9	1.3	0.12
Nest ht + Basal area	5	-65.2	140.5	1.9	0.09
Nest ht + Slope	5	-65.3	140.6	1.9	0.09
Nest ht + Blue oak	5	-65.3	140.6	2.0	0.09
Nest ht + Snag	5	-65.3	140.6	2.0	0.09
Base[3]	3	-67.8	141.7	3.1	0.05

[1] The base model for Ash-throated Flycatcher included a cubic effect of nest age.

[2] The base model for Oak Titmouse included a linear effect of nest age and a quadratic effect of nest date.

[3] The base model for European Starling included a quadratic effect of nest age.

Table 3—*Model-averaged parameter estimates, unconditional standard errors (SE), and relative importance values from logistic-exposure models relating daily survival rates of Ash-throated Flycatcher, Oak Titmouse, and European Starling nests to time-dependent and nest-site variables. For continuous variables, the sign of the estimate (Est.) indicates the effect in relation to nest success. Standard errors reflect both uncertainty in parameter estimates from a given model and uncertainty in selecting that model. Relative importance values (Rel. imp.) are the sum of the Akaike weights over all models in which that variable appears and are a measure of the relative importance of the predictor variable to daily nest survival rate.*

	Ash-throated Flycatcher			Oak Titmouse			European Starling		
Parameter[a]	**Est.**	**SE**	**Rel. imp.**	**Est.**	**SE**	**Rel. imp.**	**Est.**	**SE**	**Rel. imp.**
Intercept	5.08	3.42		47.16	20.25		13.9	4.70	
Age	0.57	0.67		0.07	0.02		-0.9	0.41	
Age^2	-0.07	0.04					0.02	0.01	
Age^3	0.00	0.00							
Date				-0.77	0.38				
Date^2				0.00	0.00				
Nest height	-0.00	0.04	0.17	0.01	0.03	0.18	0.18	0.16	0.72
Basal area	0.24	0.04	0.34	0.23	0.30	0.59	0.02	0.08	0.16
No. blue oaks	0.02	0.09	0.19	0.04	0.09	0.21	-0.02	0.07	0.16
No. live oaks	0.04	0.08	0.23	-0.00	0.03	0.18	-0.04	0.08	0.21
No. snags	0.02	0.04	0.19	-0.00	0.02	0.17	0.01	0.05	0.15
Slope	-0.00	0.01	0.20	-0.00	0.01	0.19	-0.00	0.01	0.15

[a] Age, Age^2, and Age^3 represent linear, quadratic, and cubic effects of nest age. Date and Date^2 represent linear and quadratic effects of Julian date. Basal area, number of blue oaks, and number of live oaks were log transformed.

Discussion

While the eight species studied here differed in nest habitat selection, considerable overlap occurred among some species. We found extensive overlap among nesting habitats used by European Starlings, Western Bluebirds, Violet-green Swallows, and to a lesser extent, White-breasted Nuthatches. The patterns of overlap in nesting habitat found here were consistent with those found for nest-cavity characteristics (Purcell and Verner 2007).

Niche overlap provides only weak evidence of interspecific competition without evidence of limiting resources (Wiens 1989). Results of a cavity-blocking experiment done at SJER in the mid-1980s suggested that cavities were not limiting at that time (Waters and others 1990), but numbers of starlings have increased since that study was completed (Purcell and others 2002). We suspect that nest sites have become a limited resource following the increase in starling abundance, at least for some species, based on several lines of evidence (Purcell and Verner, in review). The most compelling of these are based on observations of nest usurpation by starlings of five native species and aggressive interactions between starlings and native cavity-nesting species at nest cavities (Olsen and others 2007).

A decrease in availability of a limiting resource promotes intensified competition, which is generally believed to result in a narrowing of niche breadth or niche shifts to minimize overlap (Schoener 1982, Wiens 1989). Western Bluebirds and Violet-green Swallows had the smallest niches relative to nest habitat characteristics, as gauged by the standard deviation and range of the habitat variables measured here, suggesting decreased niche breadth. Nest-cavity variables of bluebirds and swallows also had the lowest variability compared to other cavity-nesting species in a companion study (Purcell and Verner, in review). Studies of Tree Swallows (Tachycineta bicolor), a close relative of the Violet-green Swallow, have shown them to be less selective and more variable in nest-site selection compared to other species (Dobkin and others 1995, Munro and Rounds 1985, Parren 1991, Rendell and Robertson 1989), even though access to nest sites may have been limited by competition with starlings (Dobkin and others 1995, Peterson and Gauthier 1985, Rendell and Robertson 1989).

Habitat partitioning can favor coexistence of bird species, and divergence in nesting sites can reduce predation risk (Martin 1988, Martin and Roper 1988). Bewick's Wrens were the most divergent in their nesting habitat. They also had the highest reproductive success of 16 species nesting at SJER (Purcell 1995).

Are Nest Sites Adaptive?

For nesting-habitat preferences to be adaptive, preferred sites must be more productive so that selection can act to favor preferences (Martin 1998). If successful nesting habitat differs from used nesting habitat, use might not reflect preference and could indicate niche shifts resulting from competition. Selection can only act on phenotypic variation in nest site choice if it has a genetic basis. We assumed that heritable genetic variation for habitat selection exists because a variety of evidence suggests that habitat preferences have a genetic basis (Jaenike and Holt 1991, Martin 1998).

Nesting-habitat selection by the three species examined appeared to be adaptive. Both Ash-throated Flycatchers and Oak Titmice nested and were more successful in areas with high basal area. European Starling nests were the highest of the eight species examined, and high nests were more successful, a finding in agreement with Nilsson (1984). It should be noted, however, that nesting habitat characteristics had little ability to predict nest survival of Ash-throated Flycatchers. Compared to results of a companion study examining nest-site characteristics (Purcell and Verner, in review), we found less evidence that nesting habitat was important to nest survival than were features specific to the smaller scale of the nest site. We found fewer nesting-habitat variables important in predicting nest survival and greater agreement between habitats where species nested and where they were more successful. These results suggest that optimal nesting habitat is either less limiting or less important than optimal nest sites, a question that deserves study.

Management Considerations

Habitats that are complex and heterogeneous can provide habitat requirements for greater numbers of species than simple, uniform habitats. Results of this study suggest that maintaining a diversity of habitats, including areas differing in tree density and species, can help foster wildlife species diversity. We suggest that spatially diverse and complex oak woodlands will best provide for the differing habitat needs of the species considered here.

If birds choose habitat features that increase the probability of nesting successfully, identification of these features is critical for effective management. Ash-throated Flycatcher and Oak Titmouse nests were more successful in habitat with high basal area, suggesting that high tree density and/or the abundance of large trees is important for these species. European Starlings that occupied high nests were more successful. A positive correlation between nest height and nest success has been found for a wide variety of species (Burhans and others 2002, Hatchwell and others 1999, Hooge and others 1999, Li and Martin 1991, Nilsson 1984). If species are competitively excluded from higher sites by starlings, more high-quality nest sites could be provided and competition reduced by increasing the availability of large trees. We recommend management practices that encourage maintenance of large, mature oak trees and recruitment of replacement oaks.

Although nest boxes can help reduce competition for limited nest sites, the target species and nest-box placement need to be considered. Nest boxes should be constructed to exclude starlings and monitored to assure that they are not used by non-native species. Results of this study suggest that nest boxes should be placed in appropriate habitat for each target species. A primary consideration is that not all species use nest boxes (*table 4*). The eight species considered here nested in areas that differed in tree densities and dominant tree species, and slope, and nest trees differed in species, size, and decadence (*table 4*). The needs of the entire native bird community and the potential effects of targeting a single species should be considered when augmenting existing cavities with nest boxes (Purcell and others 1997). Effects of nest box programs have rarely considered the potential effects of nest boxes on the rest of the bird community. We believe the question of community-wide effects and possible adverse impacts on other species deserves further study.

Table 4—*Summary of nesting habitat for eight cavity-nesting bird species at the San Joaquin Experimental Range.*

Species	Nest tree	Tree density	Dominant tree species	Slope	Uses nest boxes
Ash-throated Flycatcher	Large diameter live oaks	dense	Live oaks with snags	moderate	Yes
Violet-green Swallow	Tall, healthy blue oaks	medium	Blue oaks	steep	No
Oak Titmouse	Average oaks of both species	dense	Mixed	steep	Yes
White-breasted Nuthatch	Large diameter blue oaks	medium	Mixed	moderate	Rarely
Bewick's Wren	Variable	dense	Live oaks, pines, snags	steep	Rarely
House Wren	Large diameter, decadent oaks	dense	Mixed	moderate	Yes
Western Bluebird	Healthy blue oaks	sparse	Blue oaks	moderate	Yes
European Starling	Tall blue oaks	sparse	Blue oaks	level	No?

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Continue

The Response of Native Oaks From California and Israel to Drought[1]

Douglas McCreary,[2] José M. Grünzweig,[3] Yohay Carmel,[4] and Curtis H. Flather[5]

Abstract

California and Israel are both characterized by Mediterranean climates, and the native oaks growing in these two locales occupy similar ecological niches. However, in California certain oak species are having difficulty regenerating adequately, while in Israel this is not a problem. From 2004 to 2006, a series of greenhouse studies were conducted in both Israel and California to sort out the role of evolutionary history in influencing species regeneration rates and strategies. These studies have evaluated survival and growth, as well as the response of the species to disturbance including simulated browsing and fire. In 2006, an out-planting study was initiated at the University of California Sierra Foothill Research and Extension Center in Yuba County to determine how the species respond under normal field conditions. Three California oak species, including *Quercus agrifiolia*, *Q. douglasii* and *Q. berberidifolia*, as well as two Israeli oak species (*Q. ithaburensis* and *Q. calliprinos*) were planted in a common garden. This latter study was designed to evaluate phenology, growth rates, and how seedlings respond to summer drought in terms of pre-dawn plant moisture stress (PMS). Unfortunately, high field mortality prevented assessing plant moisture stress or field growth rates so the results reported here include only initial size, bud burst date and survival. Results indicate that the deciduous species from both locations (*Q. douglasii* and *Q. ithaburensis*) break bud far earlier than their evergreen counterparts. Growth in containers varied greatly by species, with *Q. agrifolia* from California and *Q. ithaburensis* from Israel growing far more rapidly that the other species. Finally, a comparison of the survival of evergreen and deciduous species from Israel with those from California suggests that California species tended to die earlier. These results are consistent with results from the greenhouse studies that found that the California species were generally less water-use efficient and might be less adapted to drought stress than Israeli species.

Keywords: Bud burst, Mediterranean climate, oak regeneration, oak survival.

Introduction

Both evergreen and deciduous oaks grow in Israel and California and are able to survive in the often-harsh Mediterranean climates that characterize both regions. While the absolute rainfall amounts vary greatly both within and between regions, both areas have a lengthy dry period from late spring until early fall. Plants adapted to these Mediterranean climates must be able to withstand drought and have evolved

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[2] Natural Resources Specialist, University of California at Berkeley, 8279 Scott Forbes Road, Browns Valley, CA 95918. email: mccreary@nature.Berkeley.edu.

[3] Faculty of Agricultural, Food and Environmental Quality Sciences, The Hebrew University of Jerusalem, Rehovot, Israel. e-mail: jose@agri.huji.ac.il.

[4] Faculty of Civil and Environmental Engineering, Technion – Israel Institute of Technology, Haifa, Israel. e-mail: yohay@techunix.technion.ac.il.

[5] Research Wildlife Biologist, USDA, Forest Service, Rocky Mountain Research Station, Fort Collins, CO, United States. e-mail: cflather@fs.fed.us.

various mechanisms to do so. However, regeneration in California is problematic as three California deciduous species (*Q. douglasii* – blue oak; *Q. lobata* – valley oak; and *Q. engelmannii* – Engelmann oak) appear to have insufficient natural regeneration in portions of their ranges to replace mortality (Muick and Bartolome 1986, Bolsinger 1988).

It is also not clear exactly what adaptive mechanisms the different species use to withstand drought and whether deciduous or evergreen species have an advantage. It may be that evergreen oaks are better suited to withstand periodic droughts in such environments since, unlike their deciduous counterparts, they can continue to photosynthesize in winter, thus avoiding activity during the extended period of drought. On the other hand, deciduous oaks have the ability to go dormant and shed their leaves under extremely dry conditions, thus preventing moisture loss and avoiding lethal desiccation.

This study is part of a larger project titled “The Role of Evolutionary History in Determining Vegetation Dynamics: A Comparative Study of Mediterranean Ecosystems in California and in Israel,” underway since 2002. The larger project was designed to compare evergreen and deciduous species from both Israel and California and to evaluate the growth and performance in a greenhouse setting, including their response to disturbance. Initial results were reported in 2004 (Carmel and Flather 2004). The study described in this report was an opportunistic tangent that allowed us to compare our greenhouse findings of seedling response (Grünzweig and others, in press) with those of seedlings outplanted to natural field conditions using extra seedlings from that larger project.

Methods

Five species were evaluated in this study. They included Palestine oak (*Q. calliprinos*), an evergreen oak from Israel; taber oak (*Q. ithaburensis*), a deciduous species from Israel; coast live oak (*Q. agrifolia*), an evergreen oak native to coastal regions of California; blue oak, a widely distributed deciduous oak endemic to California; and scrub oak, *Q. berberdifolia*, a widely distributed shrubby evergreen species native to California.

All acorns for this study were collected in their native ranges between late October and early November 2002. In California, the acorns were all collected in Carmel Valley, approximately 30 km inland from the Pacific Ocean and between 300 and 400 m in elevation. For each of the five oak species, acorns from two to three sites were collected and combined to ensure wider genetic diversity. They were sown in January 2003 at the nursery of Rana Creek Restoration in Carmel Valley, California. This area has a Mediterranean climate with long-term average annual precipitation of 534 mm with little or no rain between June and September. Acorns were initially planted in trays consisting of 34 cm^2 compartments. Seedlings were irrigated once a day and the potting soil contained a slow-release fertilizer. Seedlings also received a liquid fertilizer once or twice a week. In late February 2004, seedlings were transplanted to 15 L bags made of woven plastic synthetic fabric. The substrate used for transplanting contained medium and coarse redwood, tufa (porous stone of volcanic origin), Perlite, and slow-release fertilizer. Seedlings of each species were randomly divided into 5 or 10 groups consisting of 25 to 33 seedlings, which were then randomly placed in a shade-house. During their stay in the shade-house, the seedlings were kept well watered by overhead irrigation. In August 2005, most of the seedlings were harvested and a variety of morphological and physiological measurements were recorded, including height and basal diameter, shoot-root ratio, ratio of small roots to the taproot, and tissue nutrient concentrations. However, a subsample of 20 seedlings from each species was brought to the University of California Sierra Foothill Research and Extension Center (SFREC) near Marysville, California, for out-planting and further assessment. These seedlings were “leftover,” but were similar morphologically to those that were harvested.

These seedlings were initially placed under a white canvas, open-sided canopy and watered daily until they were outplanted in mid-February 2006. Seedlings were planted in a randomized block design with each block consisting of five 5-seedling rows, with each row containing seedlings from one of the species. Within each block, species were randomly assigned to rows. Rows were 1.5 m apart, as were seedlings within each row. Prior to planting, a hole was excavated at each planting spot to an approximate depth of 0.5 m using a 0.3-m diameter tractor-mounted auger.

All seedlings were planted in a single day and were watered-in to ensure adequate initial soil moisture, good root-soil contact, and to eliminate any air pockets. Before planting, the entire plot was treated with glyphosate to eliminate weed competition, since the density of the weeds was highly uneven within the plot and we wanted to make sure that soil moisture conditions remained as uniform as possible.

Eight days after planting, the height and basal diameter of each planted seedling were measured and recorded. Starting in March, the plants began breaking bud and leafing out. At this time, we began assessing each seedling for bud burst approximately every 10 days using the rating system below:

0 - Buds firm, no swelling,

1 - Some bud swelling, but no buds partially or fully open,

2 - Most advanced buds open and expanding, but no stem elongation,

3 - Buds fully open, some stem elongation, but leaves not yet fully expanded and formed,

4 - New leaves fully formed.

For each species and on each evaluation date, the bud-burst ratings were calculated to generate an average bud-break rating. In early June, we noticed that the leaves on some of the deciduous species were turning brown and falling off. This was noted, but we felt that is was probably the result of some dry soil conditions near those particular seedlings and these seedlings were shedding foliage to maintain a more favorable moisture status. Such drought-deciduousness has been previously observed for blue oaks during extremely dry years (McCreary 1990). At the end of June, some leaf drop was still occurring but most seedlings were still green. In early July, some seedling mortality was noted but it was still within an acceptable range. July, however, was one of the hottest months on record, and for 13 straight days the maximum daily temperature exceeded 36^{o} C, reaching a high of 42.6^{o} C on July 22 (CIMIS data). By early August, almost 90 percent of the seedlings appeared dead, precluding measurements of field growth and plant moisture stress. We expected the mortality to increase further and that few of the seedlings would either leaf out normally next spring or sprout from their base because, as noted above, the plants appeared dead. However we will assess the plot next year to determine if all of the seedlings that appear dead really are dead. While we are extremely disappointed in this turn of events, we do believe some useful information can still be gleaned from this experiment as we outline below.

Statistical Analyses

We compared seedling height, basal diameter, bud burst, and survival among species using ANOVA and Fisher's Protected Least Significant Difference (LSD) tests. The data for these analyses were the averages for the 5-seedling species rows in each replication. Unless there were significant differences ($P < 0.05$) among means in the analysis of variance, species were not considered significantly different. If there were significant differences, however, an LSD test was conducted to determine which species were significantly different ($P < 0.05$) from one another.

Results

Seedling Size

There were marked differences among species in the size of the seedlings at the time of planting, and there were significant differences among species in both height and basal diameter (*table 1*). All five species differed among each other except for *Q. calliprinos* and *Q. ithaburensis*, which did not differ in height, and *Q. berberidifolia* and *Q. douglasii*, which did not differ in diameter. There were no apparent differences related to evergreen/deciduous status or origin.

Table 1—*Average height and diameter of seedlings at time of field planting*[1]**.**

Species	Deciduous (D) Evergreen (E)	Israel (I) Calif. (C)	Avg. Height (cm)	Avg. Diam. (mm)
Q. agrifolia	E	C	116 a	20.9 b
Q. berberidifolia	E	C	44 c	9.2 d
Q. calliprinos	E	I	62 b	11.6 c
Q. douglasii	D	C	27 d	8.5 d
Q. ithaburensis	D	I	70 b	22.8 a

[1] Different letters within the height and diameter columns indicate there is a significant difference for this variable among species, according to a Fisher's Protected Least Significant Difference (LSD) test.

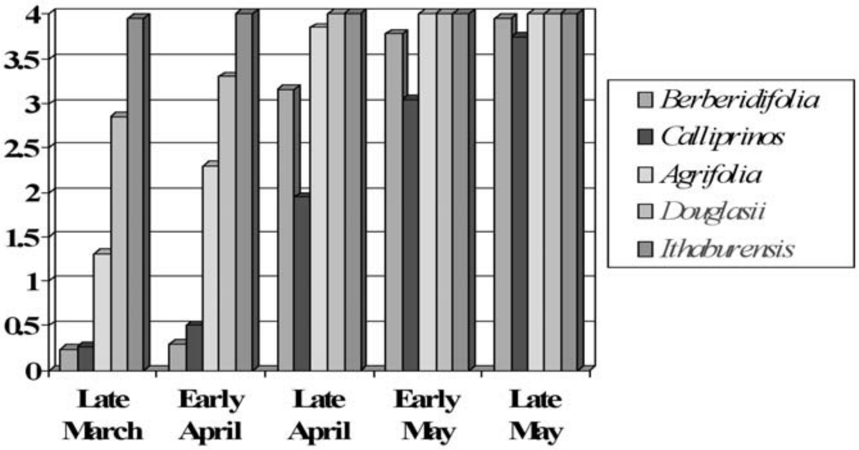

Figure 1—Bud burst averages over time for different species[1]

[1] *Quercus berberidifiolia* and *Quercus calliprinos* had significantly ($P < 0.05$) smaller bud burst ratings than the other three species on the first three evaluation dates.

Bud Burst

Species differed in bud-burst rating (*fig*. 1). As shown, the deciduous oaks from both California and Israel broke bud and began to leaf out far earlier than their evergreen counterparts. By early-April, these two species were almost fully leafed out while the evergreen species, especially *Q. berberidifolia* and *Q. calliprinos*, were just beginning to burst bud.

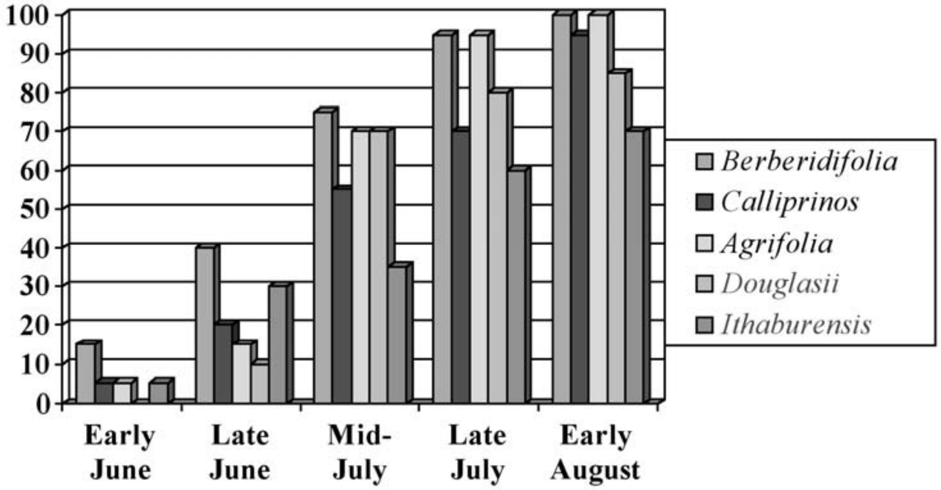

Figure 2—Average cumulative percent mortality over time for different oak species.

Mortality

Most seedlings appeared alive and well until late June (*fig. 2*). By mid-July, however, mortality had increased dramatically, and by early August nearly 90 percent of all seedlings appeared dead. However, the timing of mortality varied greatly by species. The deciduous species *Q. douglasii* and *Q. ithaburensis* survived longer than the other species and by early-August, over 20 percent of these seedlings still had green leaves, in contrast to the other three species that had a total of only two seedlings (out of 60) with some green leaves. This was the only evaluation period in which there was a significant difference among species, with *Quercus ithaburensis* having significantly lower mortality than the other four species.

Discussion

As indicated above, one of the primary purposes of this study was to compare the plant moisture stress of the different species to determine if they exhibited different strategies to deal with drought. This was not possible because of the unexpected high mortality and the lack of viable seedlings to assess. However, we were able to compare size, bud break, and survival, and gain some insights into how different seedlings perform.

Seedlings varied greatly in how much they grew while still in the planting bags. The two largest species at the time of field planting, both in terms of height and basal diameter, were *Q. ithaburensis* – a deciduous oak from Israel – and *Q. agrifolia* – an evergreen oak from California. The other three species were all fairly similar in size and included a deciduous oak from California (*Q. douglasii*), an evergreen oak from Israel (*Q. calliprinos*) and an evergreen oak from California (*Q. berberidifolia*). Clearly there was no discernable relationship between growth or size and country of origin or whether or not plants were deciduous or evergreen.

As indicated above, most seedlings appeared dead by late July. The cause of mortality is uncertain and could have been the result of the unseasonable heat, or because of the accompanying drought – or perhaps because of the “pampered” conditions the seedlings were raised in. In any case, by late July large numbers of seedlings began to turn brown and die. We felt they were not simply exhibiting drought-deciduousness because the change in leaf color was accompanied by the stems becoming extremely dry and brittle.

By late August, the two deciduous species, *Q. douglasii* and *Q. ithaburensis*, had the highest average survival. Some had lost considerable foliage, but as noted above, over 20 percent of these appeared alive. It is also interesting that these two species began breaking bud and leafing out far earlier that the evergreen oaks, regardless of origin. This would indicate that these species have evolved a strategy to take advantage of favorable environmental conditions in the early spring by developing the photosynthetic apparatus to capture the sun’s energy. These two species were at opposite ends of the size rankings when they were planted. Of all of the species, *Q. douglasii* was the smallest in terms of height and basal diameter, while the Israeli *Q. ithaburensis* had the largest basal diameter and was the second tallest of the five species. It therefore does not appear that initial size of the species at time of planting is correlated either with bud burst date or survivability.

A comparison of evergreen Israeli and California species suggests that the species from Israel had higher initial survival than California evergreen species. Further, the Israeli deciduous species (*Q. ithaburensis*) had significantly higher survival on the last evaluation date than *Q, douglasii*, its deciduous counterpart. These results are consistent with results from the greenhouse studies that found that the California species were generally less water-use efficient and might be less adapted to drought stress than Israeli species (Grünzweig and others, in press).

There was also no pattern related to country of origin and growth in containers, as by far the two largest species (*Q. agrifolia* and *Q. ithaburensis*) were from different locales. However, this does not imply that location had no effect on seedling morphology or physiology, as measurements on shade-house-grown seedlings in both Israel and California indicated that California species in general had lower seedling survival, lower water-use efficiency, greater specific leaf area and greater changes in stable carbon isotopes (Grünzweig and others, in press).

Conclusions

We detected no consistent differences between Israeli and California oak species in terms of growth in containers, bud break after out-planting, or survival in the field. This is not to say that all species performed the same, as there were substantial differences among species for all of these variables. It is just that these differences did not appear to be correlated with the location in which the species naturally grow. However, evergreen and deciduous species did respond differently after out-planting, and a comparison of the survival of evergreen and deciduous oaks from Israel with those from California does suggest that California species may be less well adapted to drought. Regardless of origin, the two deciduous species in this study broke bud far earlier that their evergreen counterparts and also survived longer under the harsh out-planting conditions. The notion that California oak species do not adapt as well to drought is speculatory and based on only five oak species and a relatively small number of seedlings within each species. These results also suggest that whether or not species are evergreen or deciduous may play a larger role in their responses to harsh environmental conditions than where they come from.

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Continue

Landscape Context Influences Bumble Bee Communities in Oak Woodland Habitats[1]

Gretchen LeBuhn[2] and Cynthia Fenter[3]

Abstract

Oak woodlands in Northern California are becoming increasingly fragmented due to increasing urban and agricultural development. Much of the change in land use in Napa and Sonoma counties has been from oak woodland to vineyards. Because bees do not use grape flower pollen, a change in landscape use from oak woodland to vineyard may have an impact on native bee communities. We examine how bumblebee, *Bombus* (Apidae), abundance and species richness are affected by oak woodland fragmentation. Adaptations such as polylectic foraging (utilizing multiple floral resources) and long flight distances may decrease the impact of fragmentation on bumblebees. The study sites, six in Napa and six in Sonoma counties, were determined to have varying percentages of vineyard in the area surrounding the sites. Collections were made at each site twice per month between March and September 2002 to 2004. Bumblebees were collected in two ways: netting and using pan traps. We found no significant difference between high and low vineyards in bumblebee abundance or richness. However, bumblebees use more exotic plants in oak woodland surrounded by vineyard.

Keywords: Bumblebee, exotic plant, fragmentation, native plant, vineyard.

Introduction

In the wine country of California, natural areas are being converted to farmland and pasturelands at a staggering rate. Between 1995 and 2000, more than 100,000 acres of land in California were converted to wine-grape agriculture (Merenlender 2000). These landscape changes in what are primarily oak woodland habitats may affect the ecological integrity of the remaining oak woodland.

When a landscape is converted to agricultural use, the remaining habitats become fragmented and with this fragmentation there can be an increase in edge habitat and, often, there is an increase in invasive plant species (With 2002). Previous work suggests that fragmentation may also cause declines in overall pollinator abundance (Jennersten 1988, Goverde and others 2002) and native bee species richness (Steffen-Dewenter 2002). Because bees do not use grape flower pollen, change in landscape use from oak woodland to vineyard may have an impact on native bee communities, either by changing the resources available to bees or by changing the ability of bees to move through the landscape. Changes in the matrix surrounding core habitats have been shown to influence the ability of other invertebrates to traverse from one site to the next (Ricketts 2001).

The majority of previous investigations regarding landscape change in oak woodlands focus on vertebrates and plants (e.g., Knapp and others 2001, Block and Morrison 1998, Hilty and Merenlender 2004). Very little is known about the possible

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[2] Assistant Professor, San Francisco State University, Department of Biology. 1600 Holloway Avenue, San Francisco, 94132.

[3] Graduate Student, San Francisco State University, Department of Biology. 1600 Holloway Avenue, San Francisco, 94132.

effects that vineyards have on invertebrate populations. Recent work on solitary bees in oak woodlands suggests that there is a decrease in species diversity and number of species in habitats dominated by vineyards (LeBuhn, in prep).

Bumblebees (*Bombus Latreille*: *Hymenoptera*) have adaptations that may allow them to persist in areas of fragmentation. Bumblebee body mass can range (depending on species and hive duty) from 0.05g to 0.6g (Heinrich 1979). Being relatively large, bumblebees can carry more nectar and pollen longer distances that other bee genera. Bumblebees are able to warm and cool themselves using their flight muscles, consequently enabling them to fly as well as forage within a greater range of temperatures than bees that do not thermoregulate (Heinrich 1979). Bumble-bees are polylectic foragers, and therefore may make use of exotic invasive plants species that are a result of increased edges in fragmented habitats.

As part of a larger study on the impact of landscape change on the flora and fauna of Napa and Sonoma counties, we examined population abundance and species richness in oak woodland wild areas surrounded by different percentages of vineyard to determine to what extent bumblebees are impacted by the surrounding vineyard matrix. We also examined whether bumblebees utilize native plants and exotic plants differentially.

Methods

Study Organisms

Bumblebees are eusocial insects that live in colonies founded by a single over-wintering queen. The queen forages for nectar and pollen in early spring to provide for her early brood members. Once the nest is established, workers take over the task of foraging for the colony through the season. In mid- to late summer, new queens and males are produced. The new males and reproductive queens leave the nest to mate, and the new queens search for appropriate quarters for hibernation. The six bumblebee species (*B. vosnesneskii, B. californicus, B, sitkensis, B. melanopygus, B. bifarius, and B. flavifrons*) that we observed in Napa and Sonoma counties are ground-nesting, generalist foragers that use a variety of floral resources; *Bombus spp.* were observed using both native and non-native plants at all sites.

Sites

To evaluate the abundance and species richness of bumblebees, and to determine whether there is a significant difference between native or exotic floral resource use in fragmented oak woodlands, we chose sites using aerial photographs and GIS maps of the Napa and Sonoma valleys. Potential study sites all met certain criteria for low elevation (100 to 200m) and slope (5 to 15°) to reduce variance between sites. We analyzed the percent of land that is vineyard within 1,000 m of each potential site. Surrounding areas composed of greater than 35 percent vineyard were defined as ‘high’ vineyard and areas with less than 10 percent vineyard were defined as ‘low.’ We visited each potential sampling site and included all sites that had at least 1 ha of oak woodland and that we were able to get permission to sample.

Sampling

We followed standard bee sampling techniques (protocols can be found at http://online.sfsu.edu/~beeplot). Within each site a 100 m2 sample plot was established. Collections were made at each site twice per month between March and September in 2002, and between April and September 2003. Bumblebees were sampled using nets and pan traps. Preliminary data and previous monitoring studies show different colored pan traps attract different species of bee (Leong and Thorp 1999). Therefore, we used 30 plastic Solo Brand® bowls that were 5-in., 6-oz.—10 bowls each of white, blue, and yellow for each transect. The blue and yellow bowls were painted with Krylon® fluorescent paint. The bowls were divided into sets of 30 (10 of each color) and numbered so that we could randomize the order of the colors. Each bowl was placed 5m apart along two transects in each plot. The bowls were filled with a stock solution of one teaspoon of Dawn® dish detergent per gallon of water to reduce water surface tension in the pan traps. Bowls were set out between 09:00 and 15:00h. Bees caught in pan traps were pinned and identified to species.

We netted bumblebees for 1 hour in the morning and 1 hour in the afternoon per sampling day. We divided each sampling plot into quadrants and netted within each quadrant for 15 minutes. The host plant type being utilized by the bee at the time of sampling was identified to species. At least one voucher specimen was taken of each bumblebee and plant to verify identification. In 2002, to assess the availability of floral resources, we identified to species (where possible) and measured the number of open flowers per sampling event to the greatest order of magnitude (1, 10, 100, 1k, 10k, 100k, 1m, 10m).

Analysis

To determine if there is a significant difference between 'high' and 'low' vineyard sites in bumblebee abundance and species richness, net data and pan trap data were pooled and analyzed using a two-way ANOVA using SPSS (ver. 11.5). To examine the relationship between host plant type and vineyard effect across both sampling years, we created contingency tables using Statview (ver. 5.01)

Results

We found 6 species of the 12 distinct species of bumblebees reported in Napa and Sonoma counties. They were from highest to lowest frequency (2002 sample / 2003 sample): *B. vosnesenskii* (604/210), *B. californicus* (49/80), *B. melanopygus edwardsii* (16/64), *B. flavifrons* (1/5), *B. bifarius* (0/4), and *B. sitkensis* 0/1). *B. vosnesenskii* was the most abundant species across all sites and years. There were three species on average in both high and low vineyard sites in 2002 and 2003. We had significantly higher numbers of bumblebee observations overall in 2002 (670) relative to 2003 (389).

We found no difference in the richness or abundance (*table 1*) of bumblebees between sites surrounded primarily by vineyard and sites embedded in a natural landscape in either year.

Table 1—*Two-way analysis of variance of natural log of species richness and natural log of abundance.*

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Species Richness					
Year	0.001	1	0.001	0.011	0.917
Vineyard	0.007	1	0.007	0.064	0.803
Year*Vineyard	0.171	1	0.171	0.159	0.221
Abundance					
Year	1.490	1	1.490	1.674	0.210
Vineyard	2.531	1	2.531	2.843	0.107
Year*Vineyard	0.505	1	0.505	0.567	0.460

In addition, we found that bumblebees were using native plants less frequently than exotic species in both the high and low vineyard sites in 2002 and 2003 (*figure 1*, 2002: X^2=3.928, p-value = 0.0475, 2003: X^2=7.871, p-value = 0.005). In 2002, there were 216 observations of bumblebees on exotic species and 57 on native species in high vineyard sites, and 294 observations of bumblebees on exotic species and 38 on native species in low vineyard sites. In 2003, there were 123 observations of bumblebees on exotic species and 47 on native species in high vineyard sites, and 96 observations of bumblebees on exotic species and 14 on native species in low vineyard sites.

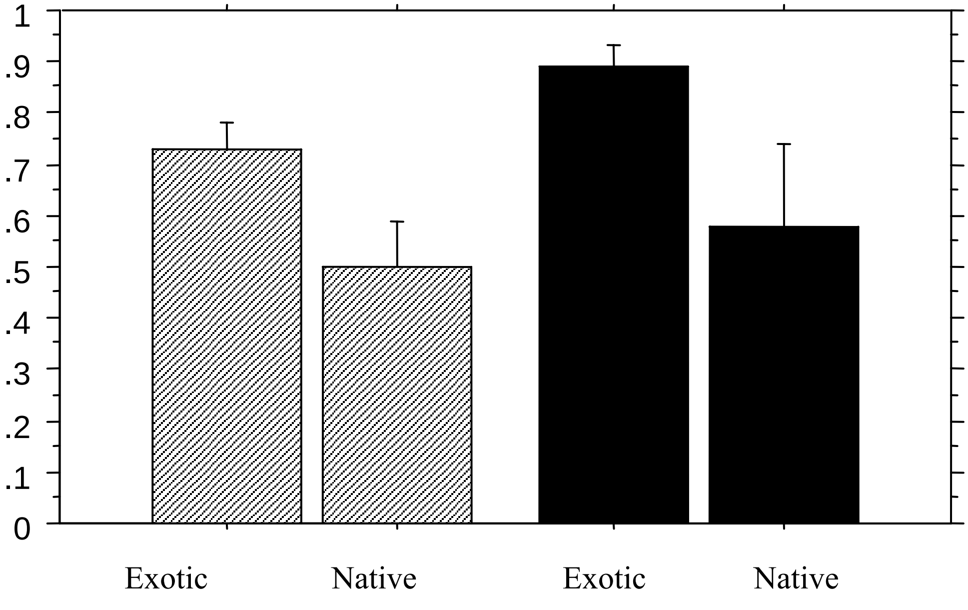

Figure 1—Proportion of bumblebee visits to exotic or native host plant in 2002. Striped bars are in a high vineyard environment. Solid bars are in a low vineyard environment.

Discussion

Our results indicate that there was no difference in the richness or abundance of bumblebees between sites surrounded primarily by vineyard and sites embedded in a natural landscape. This is not to say that fragmentation or landscape conversion is beneficial, it only underlines how remarkably adaptive some organisms are in the face of abrupt modification of their surrounding landscape.

Landscape change is one cause of fragmentation, which may decrease bee abundance and species richness (Jennersten 1988, Steffen-Dewenter and Tscharntke 2002, LeBuhn unpublished data). However, other work suggests that certain species of native bees can thrive in a fragmented landscape depending upon foraging behavior and nest site availability (Cane 2001, Steffen-Dewenter 2002).

We found that the most common species, of the six that we observed, at all sites were *Bombus vosnesenskii*, *Bombus californicus* and *Bombus melanopygus var. edwardsii* and that there were three species on average in both ‘high’ and ‘low’ vineyard sites. On record, there are 12 distinct species of *Bombus* in Napa and Sonoma counties (R. Thorp pers. comm.). It may be that although there remains some contiguous wild area in these valley oak woodlands, overall species richness is low on a larger landscape scale than this study measures. McFrederick and LeBuhn (2006) found that bumblebees in urban parks in San Francisco are experiencing low species richness as compared to surrounding wild areas. This suggests that the loss of certain species in fragmented areas may be due to interspecies competition. More work on competition effects between species of bumblebees within urban parks as well as fragmented oak woodlands may uncover the effects of interspecies competition on species richness in fragmented landscapes.

One explanation for bumblebees showing no marked change in numbers between sites is that they do not experience the sites as fragments. The adaptive physical and behavioral characteristics that allow bumblebees to be unaffected by landscape change may be due to their greater foraging abilities. *Bombus spp.* foraging distances can range from 50m to 80km in extreme cases (Mikkola 1984), with averages around 350m (Dramstad 1995, Osborne and others 1999). Davies and others (2000) found that, species that experience isolation due to fragmentation are at greater risk for declines in population. Their larger body size, thermoregulation and generalist foraging habits may allow them to nest in one fragment and find suitable host plants in a number of other fragments.

Bumblebees need two resources to persist in a given habitat: floral resources and nesting sites. As relatively long-lived, generalist foragers, bumblebees are able to use a wide variety of floral resources, but those resources must persist throughout the foraging season. Interestingly, after July 1, 2002, nearly all host plants visited by bumblebees were exotic, even though 30 percent of the plants in bloom after July 1 were native (Fenter and LeBuhn in prep.).

It is possible that the length of the foraging season for bumblebees may be extended artificially by these non-native plants, an unexpected positive benefit of the expansion of exotic plant species. This study does not make the claim, however, that invasive species are utilized at an equal or greater frequency than native species due to any preference, rather, that due to a greater likelihood of invasive plant species later in the season, bumblebees are utilizing these available resources. These results suggest that the biology of a particular species of *Bombus* will influence the response of that species to landscape change and that there may be a correlation between foraging behavior and fitness in fragmented oak woodland.

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Continue

Role of Hardwood in Forming Habitat for Southern California Steelhead[1]

Lisa C. Thompson,[2] Jenna L. Voss,[2] Royce E. Larsen,[3] William D. Tietje,[4] Ryan A. Cooper,[3] and Peter B. Moyle[2]

Abstract

Large wood (LW) is known to be very important to fish habitat in conifer-dominated streams of the Pacific Northwest, but has not been well studied in hardwood-dominated streams of the central California coast. In July and August 2006, we studied the occurrence and function of hardwood LW in relation to stream habitat and threatened steelhead (*Oncorhynchus mykiss*) distribution in the hardwood-dominated Upper Salinas River watershed in central-coastal California. We sampled 15 sites located on four tributaries and on the main stem of the Salinas River. At each site, we measured the volume of fallen dead LW (logs, root wads), standing trees, and not-standing live wood (exposed roots, living fallen trees) within the bankfull width. Fish density and length were estimated by a snorkel survey. Willow (*Salix* spp.), oak (*Quercus* spp.), California sycamore (*Platanus racemosa*), and Fremont cottonwood (*Populus fremontii*) dominated the sites. Fallen dead LW volume within the bankfull width averaged 47.6 m^3/ha (SD =58.2) across all sites. Total LW volume, including fallen dead, not-standing live wood, and standing live and dead trees averaged 222.0 m^3/ha (SD = 173.7). Fallen dead LW volumes on the central coast were almost 16 times less than conifer-dominated sites in the Pacific Northwest, but similar to volumes on private hardwood-dominated north coast sites. At 13 sites at least half the pools were formed due to LW, or experienced some influence of LW. An average of 4.01 fish/m (SD = 3.08) were observed at 14 sites. Steelhead were observed at 9 sites, averaging 0.23 fish/m across 14 sites (SD = 0.35). Hardwood LW appears to be an important component of steelhead habitat in central-coastal California streams, due to its influence on pool formation.

Keywords: Fish habitat, hardwood, large woody debris, Oncorhynchus mykiss*, pools, rainbow trout, steelhead, Salinas River.*

Introduction

Large wood (LW) plays a key role in the creation and maintenance of fish habitat in small coastal streams in the Pacific Northwest (McMahon and others 1996, Naiman and others 1998). LW, defined as pieces of wood with length ≥1 m, and diameter ≥10 cm, influences channel geomorphology by stabilizing channels and trapping gravel that fish use for spawning. LW is also used as habitat by macroinvertebrates, important food for fish. Pools often form under logs that have fallen into a stream, or immediately upstream of wood jams.

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[1] An abbreviated version of the paper was presented at the Sixth California Oak Symposium: Today's Challenges, Tomorrow's Opportunities, October 9-12, 2006, Rohnert Park, California.

[2] Specialist in Cooperative Extension, Junior Specialist, and Professor, respectively, Wildlife, Fish, and Conservation Biology Department, University of California, Davis 95616. e-mail: lcthompson@ucdavis.edu; jlvoss@ucdavis.edu; pbmoyle@ucdavis.edu.

[3] Area Watershed/Natural Resource Advisor, and Farm Advisor Assistant, respectively, University of California Cooperative Extension, San Luis Obispo County. e-mail: relarsen@ucdavis.edu, racooper@co.slo.ca.us.

[4] Specialist in Cooperative Extension, Integrated Hardwood Range Management Program, University of California, Berkeley. e-mail: wdtietje@nature.berkeley.edu.

Most studies of LW have been conducted in areas dominated by coniferous forest, such as the Pacific Northwest and the northern California coast. A notable exception is the work by Opperman (2005) in which LW was surveyed in hardwood-dominated watersheds in Northern California (Mendocino, Sonoma, Marin, Contra Costa and Alameda counties). He found that LW loading (volume per unit area of stream) was consistently lower than that observed in conifer-dominated systems. Nevertheless, hardwood LW still formed channel-spanning wood jams that contributed to the formation of pools. Streams he sampled on public lands had consistently higher LW loading than streams on private land, suggesting that land management practices may affect the volume of LW and, in turn, the quality and quantity of habitat available for anadromous salmonids. Hardwood LW tends to have a shorter residence time in streams than coniferous LW, potentially because it decays and disintegrates at a faster rate than coniferous LW (Hyatt and Naiman 2001). Consequently, in hardwood-dominated systems there is a need to achieve higher rates of recruitment from the riparian zone to ensure adequate instream loading. Because recruitment is determined by both riparian stand conditions and land management practices, it is especially important that landowners be informed about LW's crucial role in conserving fish habitat.

Pools are the primary refuge for steelhead (*Oncorhynchus mykiss*)[5] and other anadromous salmonids during hot weather in northern California (Nielsen and others 1994). Pool spacing is a decreasing function of LW abundance in small, coastal streams in British Columbia (Rosenfeld and Huato 2003). The role of LW in streams is known to vary with stream size, with LW having a stronger influence in small streams (Gurnell and others 2002). The LW pieces in a small stream are relatively large in comparison with the bankfull width and are therefore more likely to form wood jams and pools. Beechie and Sibley (1997) showed that the size of LW pieces that formed pools in northwestern Washington streams increased with increasing channel width, and that pool spacing was a function of the interaction of LW abundance and channel slope. LW played a large role in the formation of 63 to 74 percent of pools in streams of the conifer-dominated Pacific Northwest (Andrus and others 1988, Carlson and others 1990, Fausch and Northcote 1992, Montgomery and others 1995). Similarly, LW formed 76 percent of pools in Colorado streams in conifer-dominated old-growth subalpine forest (Richmond and Fausch 1995). In contrast, less than 15 percent of pools in streams in the mixed-wood forest of the Boreal Shield in Ontario, Canada, were formed or influenced by LW, likely due to the small size of boreal trees, and the resulting small average size of the LW pieces (mean diameter= 16.7 cm, SD = 1.6) (Kreutzweiser and others 2005). In northern hardwood forest streams in the Adirondack Mountains, wood influenced only about 5 percent of pools (Kraft and others 2002).

The Salinas River and its tributaries have been designated by the National Marine Fisheries Service as critical habitat for steelhead, listed as "threatened" under the Federal Endangered Species Act. The watershed is part of the south-central California Coast Evolutionarily Significant Unit (ESU) for steelhead. The upper watershed is in San Luis Obispo County, where 70 percent of the land is privately owned. Agriculture, including vineyards, dryland farming, row crops and cattle production, is the dominant land use. The river experiences elevated rates of bank

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[5] Steelhead and rainbow trout are the same species, *Oncorhynchus mykiss*. Steelhead are the anadromous, that is, ocean-going, form of the species. For the remainder of this paper we will refer to all *O. mykiss* as steelhead.

erosion and significant loads of sediment, nutrients, pesticides and other pollutants, possibly as a result of land use. The steelhead in the Nacimiento River, San Antonio River, and upper Salinas River (south of San Miguel) are believed to form one of three discrete populations in the Salinas Basin, the other two being in Gabilan Creek and Arroyo Seco (Boughton and others 2006). The populations are expected to have relatively low stray rates of spawners from one to another, and as such, to have relatively small rates of genetic exchange between populations. We chose to focus on the upper Salinas River watershed because spawning steelhead can still migrate to this area, while the Nacimiento and San Antonio rivers have impassable dams.

Information on fish habitat and steelhead abundance is scarce for the California central coast and, prior to this study, virtually non-existent for the upper Salinas River. We conducted this study to provide an estimate of LW loading in the watershed for comparison with other published accounts of LW loading for streams dominated by coniferous or hardwood riparian forests. We surveyed the fish community to determine the distribution and density of steelhead and other native fish species as well as to determine the occurrence of non-native fish species. Finally, we examined the role of hardwood LW in forming pools.

Methods

Study Sites

We studied 15 sites within the upper Salinas River watershed mainstem and 4 tributaries (4 sites on the mainstem Salinas River, two on Atascadero Creek, one on Rinconada Creek, five on Trout Creek, one on Tassajera Creek, and two on Santa Margarita Creek) (*fig. 1*). Because Tassajera Creek is a tributary to Santa Margarita Creek, we considered them to be one tributary to the mainstem Salinas River. Twelve sites were on private land and three were on public land. Land cover at the sites included hardwood forest, hardwood rangeland, and urban. Sites ranged in elevation from 213 to 448 m.

Surveys of each site were conducted between July 5 and August 10, 2006, when temperatures normally are at the annual maximum, and therefore most limiting to the distribution of cold-water fish such as steelhead. Flows in the upper Salinas River tend to be low at this time of year, and averaged 0.097 m^3/s (SD = 0.077) for the 14 sites that had water. The 15th site was dry throughout the study period.

Large Wood and Riparian Habitat Sampling

At each site one reach approximately 300 m long, the experimental unit, was marked using a hip chain. Reach length delineation was conducted prior to wood surveys and in conjunction with fish snorkel surveys. Six measurements of bankfull width were made at approximately 50-m intervals, following the protocol of Harrelson and others (1994). Site elevations and locations were determined with a handheld Global Positioning System (Garmin 72™).[6]

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[6] The use of trademarked equipment in this study does not imply endorsement by the University of California.

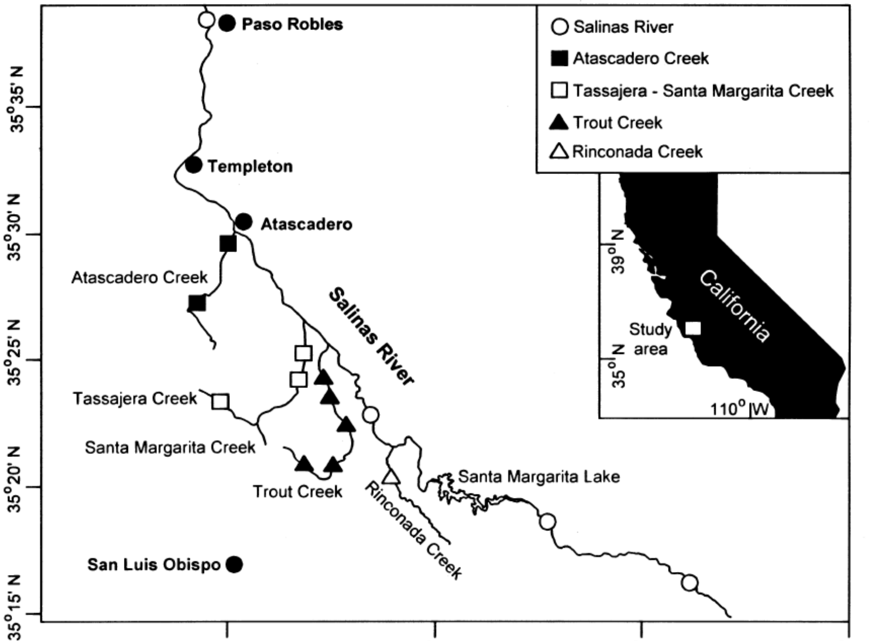

Figure 1—Map of the Upper Salinas River watershed showing sample sites on the mainstem Salinas River and four tributaries.

Studies of large wood and stream habitat in more northern regions have focused upon fallen dead wood, often termed large woody debris (LWD). However, we frequently observed standing trees within the bankfull width, and also observed live trees growing or fallen horizontally, and exposed live roots that functioned similarly to fallen dead wood pieces. We enumerated all trees and pieces in the bankfull width that met the large wood criteria, in order to determine the prevalence of standing trees, horizontal live trees, and roots relative to LWD in these south-central California sites. Large wood was categorized as fallen dead LW, not-standing live LW (live trees growing or fallen horizontally, exposed live roots), standing LW (both live trees and snags), and other LW (pieces of wood that did not fit the other categories; for example, a piece for which we could not determine whether it was alive or dead). For three pieces of wood in the fallen live and standing categories (out of a total of 953) it was not possible to determine status as standing or fallen. These pieces were included in the calculation of total LW but excluded from calculations in which wood was separated into fallen live and standing categories.

At each site, within the bankfull width, we measured the volume of wood in each category that met the LW criteria. LW was defined as a piece of wood with length ≥1 m, and diameter ≥10 cm. We measured diameter at the midpoint if the piece was fallen, and diameter at breast height (DBH) if it was standing. We also measured length, species (if identifiable), distance along the reach, channel position (bank, partially spanning, spanning), angle to stream flow, input source, input mechanism, input distance, state of decay, relationship to wood jams, relationship to pool formation, and function (formed pool, caused wood jam, stabilized bank, provided cover, aided riparian regeneration, stored sediment, or scoured the bank). The height of standing trees from the base to the point at which all branches were less than 10-cm diameter was measured with a clinometer (Haglof Electronic Clinometer

- Metric Degrees™). To obtain a more accurate estimate of wood volume for trees with major branches that grew horizontally or bent back toward the ground (for example, some *Quercus* sp. and *Salix* sp.) we measured the length of branches using a 5-m stadia rod. We calculated the volume for each piece of LW using the formula, $v = l\pi r^2$, where v = volume, l = length, and r = radius = diameter/2.

Instream Habitat Sampling

For each pool at each site, we measured length, maximum width, maximum depth, noted pool type (plunge pool over boulder, mid-channel, lateral scour, dammed, meander) and recorded the degree of LW influence on pool formation. Pools were considered (1) caused by LW, (2) enhanced by LW – LW caused an existing pool to be deeper, or to have overhanging banks, (3) influenced by LW – wood provided shade and cover, or (4) no influence of LW – the pool was formed by bedrock or lateral scour of sediment on a meander bend.

Fish Snorkel Sampling

A single pass snorkel survey of each site was conducted by one person, beginning at the downstream end of the site and moving upstream. For some run sections in which depths were less than 10 cm and algae reduced visibility, schools of small minnows and suckers were sampled by visual observation from the stream bank to avoid repeatedly counting the same individuals. Fish were identified to species whenever possible. To ensure consistency of counts and species identification, the same person conducted the snorkel survey at all sites.

Data Analysis

Raw data were entered into Excel™ and tables transferred to an ACCESS™ database. Descriptive statistics were calculated in S-Plus™ (Insightful Corporation 2001), and graphics were developed in Excel and SigmaPlot™.

Results

Fourteen tree species were identified at one or more of the fifteen study sites. Willow (*Salix* spp.), oak (*Quercus* spp.), California sycamore (*Platanus racemosa*), and Fremont cottonwood (*Populus fremontii*) were dominant (*table 1*).

Fallen dead LW volume within the bankfull width averaged 47.6 ^{m3}/ha across the 15 sites (SD = 58.2). The volume of not-standing live wood averaged 15.0 ^{m3}/ha (SD = 11.2). Standing live and dead trees contributed a high volume within the bankfull width (*fig. 2*). The volume of standing LW averaged 159.4 ^{m3}/ha (SD = 172.4). We counted an average of 31 standing trees within the bankfull width at each site (SD = 21). When averaged within site, and then across sites, the average volume of each standing tree was 2.69 ^{m3} (SD across sites = 3.36). At several sites, such as Salinas_1, Tassajera-Santa Margarita_2, Tassajera-Santa Margarita_3, and Trout_3, specimens of *P. racemosa* and *Q. lobata* with very large DBH contributed to the volume of standing LW. Total LW volume averaged 222.0 ^{m3}/ha (SD = 173.7).

Table 1—*Tree species observed at 15 sites in the upper Salinas River watershed.*

Genus	Species	Common name
Acer	*macrophyllum*	Bigleaf maple
Acer	*negundo*	Boxelder
*Alnus**		Alder (White or Red)
Fraxinus	*velutina*	Velvet (or Arizona) ash
Juglans	*californica*	California black walnut
*Pinus**		Pine
Pinus	*sabiniana*	Grey pine
Platanus	*racemosa*	California sycamore
Populus	*fremontii*	Fremont cottonwood
*Quercus**		Oak
Quercus	*agrifolia*	Coast live oak
Quercus	*douglasii*	Blue oak
Quercus	*lobata*	Valley oak
Salix	*laevigata*	Red willow
Salix	*lasiolepis*	Arroyo willow
Sequoia	*sempervirens*	Redwood
Umbellularia	*californica*	California laurel

*Indicates LW identifiable to genus only.

Trout Creek provided the most complete set of sites along an altitude gradient. Fallen dead wood volume was highest at the more upstream sites, and declined as the creek descended to the lower gradient valley floor at Trout_3 (*fig. 2*). The large volume of standing wood at Trout_3 was composed mainly of mature California sycamore. Live trees at Trout_4 were mainly willows with DBH less than the LW criterion, resulting in low values in both the standing LW and not-standing live LW categories. Standing trees at Trout_5 were mainly red willow.

We assessed the proportion of pools at each site for which (1) LW was the primary cause of the pool, (2) LW contributed to pool formation, or enhanced the habitat value of an existing pool, or (3) LW had no influence on the pool (*table 2*). Because site Trout_3 was dry throughout the study it was excluded from this assessment. At five of fourteen sites the majority of the pools were formed primarily by LW. At an additional four sites LW enhanced pool formation or influenced pool habitat value for a majority of pools. At least half the pools experienced some influence of LW at thirteen of fifteen sites. Salinas_3 was the only site at which the majority of pools were not influenced by LW.

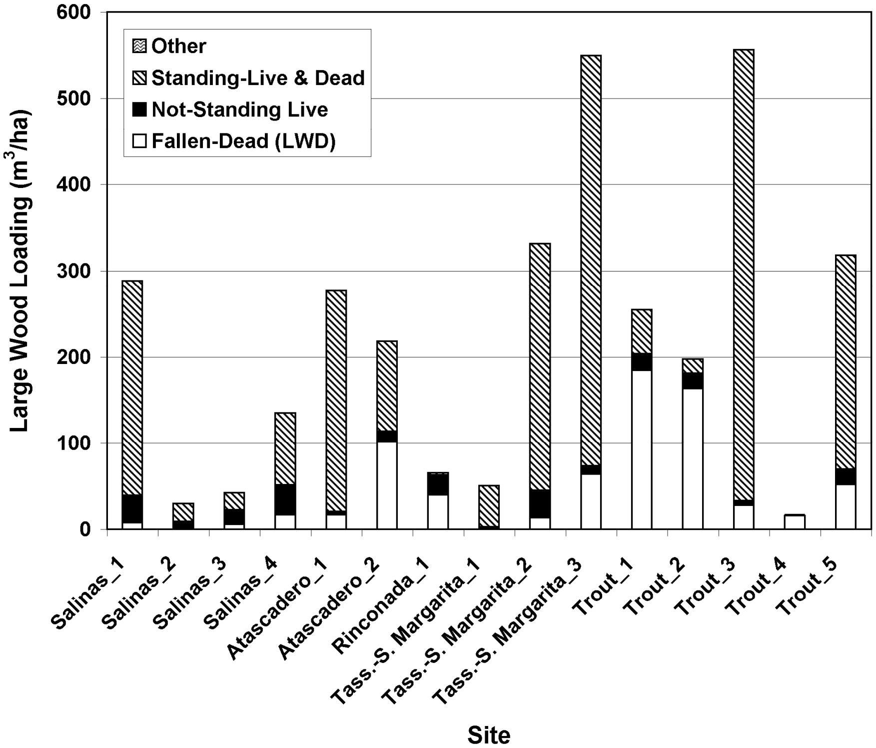

Figure 2—Loading of large wood at 15 sites in the upper Salinas River watershed. Within each tributary and the mainstem Salinas River, the sites are numbered from upstream to downstream with 1 being the most upstream site. The fallen dead category corresponds to the large woody debris category commonly used in more northern regions.

Table 2—*Role of LW in the formation of pools in the upper Salinas River watershed.*

Site	Number of Pools (pools/100 m)	Pools Formed Primarily by LW (%)	Pools Enhanced or Contributed to by LW (%)	Pools Uninfluenced by LW (%)
Salinas_1	0.30	0	100	0
Salinas_2	0.91	33.3	33.3	33.3
Salinas_3	1.60	40	0	60
Salinas_4	0.33	100	0	0
Atascadero_1	1.33	25	75	0
Atascadero_2	1.29	75	0	25
Rinconada_1	0.56	50	0	50
Tass.-S. Margarita_1	0.96	0	66.67	33.3
Tass.-S. Margarita_2	1.37	60	40	0
Tass.-S. Margarita_3	1.26	25	75	0
Trout_1	2.00	0	50	50
Trout_2	0.95	66.67	33.3	0
Trout_4	1.28	50	25	25
Trout_5	2.56	66.67	22.2	11.1

Fish were observed at all fourteen sites with water. We observed seven native and six non-native fish species (*table 3*). Between one to seven native species were seen at a given site, and between zero to five non-native species (*fig. 3*). Salinas_1 had only one identified native species, Sacramento sucker, while Tassajera-Santa Margarita_1, Trout_1 and Trout_2 had only steelhead.

Table 3—*Native and non-native fish species observed in the upper Salinas River watershed.*

Native		Non-native	
Catostomus occidentalis	Sacramento sucker	*Ameiurus* sp.	Bullhead
Gasterosteus aculeatus	Threespine stickleback	*Cyprinus carpio*	Carp
Lavinia exilicauda	Hitch	*Lepomis cyanellus*	Green sunfish
Lavinia symmetricus subditus	Monterey roach	*Lepomis macrochirus*	Bluegill
Oncorhynchus mykiss	Rainbow trout / steelhead	*Micropterus dolomieu*	Smallmouth bass
Ptychocheilus grandis	Sacramento pikeminnow	*Micropterus salmoides*	Largemouth bass
Rhinichthys osculus	Speckled dace		

Total fish density averaged 4.01 fish/m (SD = 3.08) (*fig. 4*). Native fish density, except steelhead, averaged 3.02 fish/m (SD = 2.94), while non-native fish density averaged 0.04 fish/m (SD = 0.14). The highest proportion of non-native fish occurred at Salinas_3. Unidentified fish were usually minnows smaller than 6 cm and were difficult to identify to species.

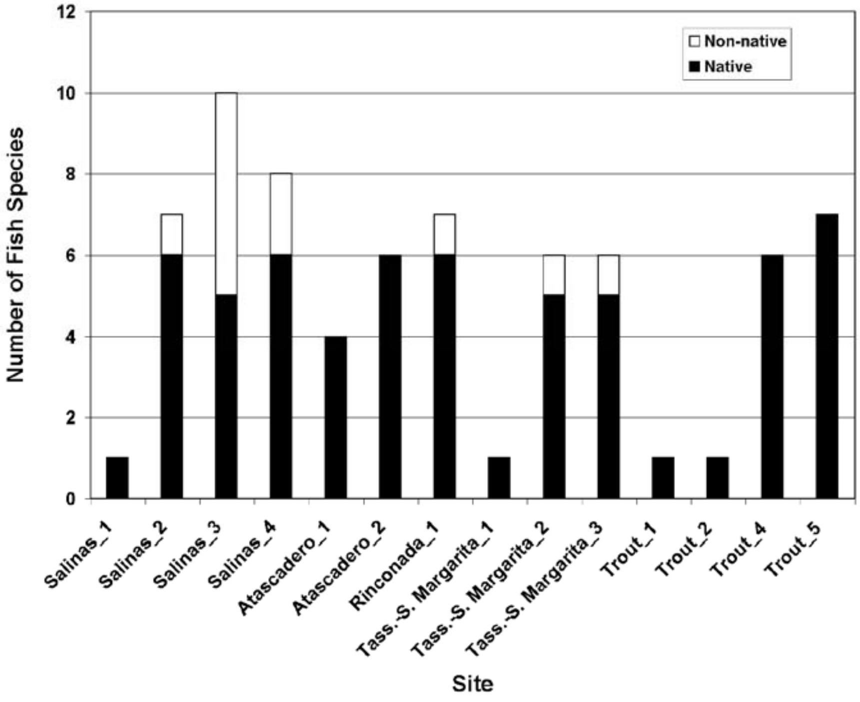

Figure 3—Number of native and non-native fish species observed at 14 sites in the upper Salinas River watershed.

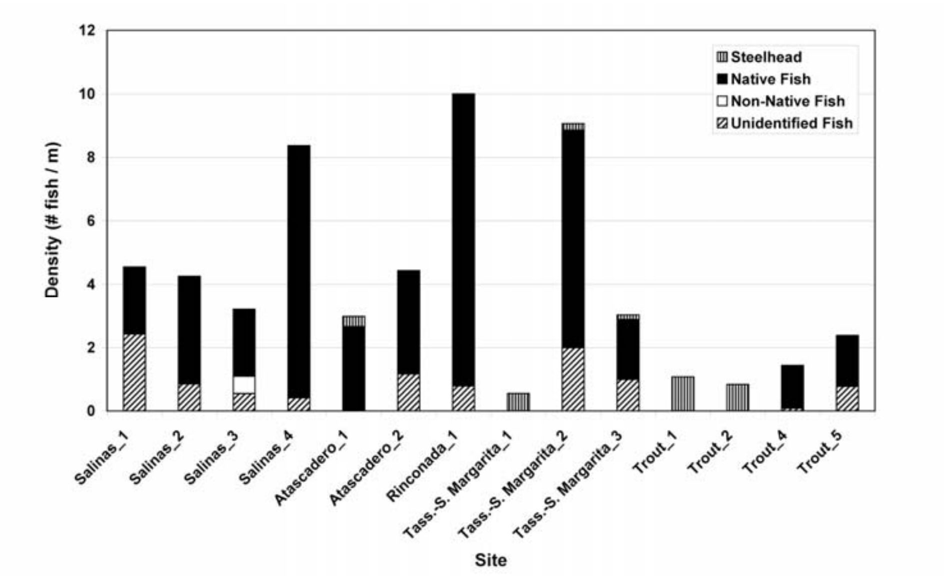

Figure 4—Density of steelhead, other native, non-native, and unidentified fish at 14 sites in the upper Salinas River watershed.

Steelhead were observed at nine out of fourteen sites (*fig. 4*), averaging 0.23 fish/m (SD = 0.35). Steelhead densities at Atascadero_2, Trout_4, and Trout_5 were 0.327 fish/m, 0.016 fish/m, and 0.003 fish/m, respectively, and are thus difficult to discern in the figure. Steelhead were not observed at any mainstem sites during the regular snorkel surveys. One steelhead juvenile was observed during a preliminary survey of Salinas_3 on July 13, 2006. However, when the full snorkel survey was conducted on August 10, 2006, no steelhead were observed.

Discussion

Hardwood LW appears to have an important impact on fish habitat in our study sites. LW was responsible for the formation of a majority of pools at about one-third of our sites, and was influential in forming pool shape or providing overhead cover at another third of the sites. The presence of hardwood LW is improving fish habitat in this watershed through its influence on pool formation and function.

A large component of LW within the bankfull width was composed of standing trees at our study sites. This contrasts with the conceptual model of conifer-dominated streams in the Pacific Northwest, in which the channel contains mainly fallen dead LW as opposed to standing trees (Naiman and others 1998). In these northern streams, the channel bed comprises a large proportion of the bankfull width and is wet for most of the year (Pollock 1998). Standing trees may be more likely to be present within the bankfull width in streams on the southern-central California coast due to the Mediterranean climate. For example, the Salinas River experiences a large difference between summer base flows and annual maximum flows, with nearly 90 percent of the annual precipitation falling between November and April (Farnsworth and Milliman 2003). Winter storms often cause large flows for short periods of time and result in bankfull widths that are large in comparison with summer wetted widths. Saplings can become established within the bankfull width channel during the extensive low-flow periods. In our study sites, the roots of trees within the channel were often exposed and were frequently associated with pools. It appears that scouring around the roots during high flows may hollow out pools. At some sites, these pools were the last refuges for fish as the water dried up (e.g., Salinas_1).

Standing trees within the bankfull width only interact with the stream up to the bankfull depth, so the full volume of a standing tree may overestimate its role relative to fallen dead LW volume. However, standing trees may be particularly important in forming fish habitat in south-central coastal streams due to their ability to anchor wood jams. While fallen dead LW pieces may form the key piece in a jam, the rapid decay rate of hardwood may make these jams short lived. A jam anchored by a standing tree is likely to be more persistent in a hardwood-dominated system. Standing trees within the bankfull width are also very likely to fall within the bankfull width once they die, contributing to fallen dead LW.

Native fish species were present at all 14 sites with water. Non-native fish species were in lower abundance than natives at all sites. The number of native species tended to increase downstream along the mainstem and along each tributary, potentially due to changes in gradient, velocity, and temperature. Native species less adapted to cooler temperatures and higher velocities may have been excluded from the cooler, higher gradient sites. Non-native species tended to be observed at the more downstream sites on the mainstem and tributaries. Sites with non-native species were generally warmer and had lower flow velocities[7], which may have allowed non-native species to compete more readily with native species. Sites with steelhead tended to have cooler water temperatures and be located at the upstream, higher elevation end of each tributary. Young-of-the-year steelhead were usually observed in shallow riffles over a gravel bottom, while juvenile steelhead were observed in deeper water such as runs or pools. Adult steelhead were usually observed in pools, and under large wood. Steelhead were present at nine sites (64 percent). This may represent the minimum distribution of steelhead across these sites in 2006, because our sampling was done at the hottest time of the year when we would expect steelhead to be restricted to the coolest locations, and to be using refugial habitat such as deep, cool pools.

Sites in the upper Salinas River watershed had loadings of fallen dead LW comparable to privately owned sites studied by Opperman (2005) in Northern California (*table 4*). Mean loading was one third that of conifer-dominated Sierra Nevada sites, and only one-sixteenth that of conifer-dominated sites in the Pacific Northwest. While it may be unreasonable to expect hardwood-dominated areas to contribute the volume of LW possible in conifer forests, average volumes at our predominantly private sites were less than half that of hardwood-dominated public sites (e.g., protected watersheds within parks) studied by Opperman (2005) in Northern California.

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[7] Unpublished data, Lisa C. Thompson, Wildlife, Fish, and Conservation Biology Department, University of California, Davis, California.

Table 4—*Comparison of instream LW loading (m^3/ha) across regions of western North America.*

Region	n	Mean (SD)	Median (interquartile)	Maximum
Pacific Northwest (BC, WA, OR)[a]	62	752 (810)	535 (315, 858)	4500
Sierra Nevada conifer[b]	12	160 (99)	159 (108, 209)	=382
No. CA hardwood, protected watersheds[c]	9	115 (33)	107 (93, 137)	=173
No. CA hardwood, private land[c]	23	42 (43)	20 (14, 59)	=146
So. CA hardwood (this study)	15	47 (58)	17 (11, 58)	=164

[a] Data from Andrus and others (1988), Harmon and others (1986), and Keller and Tally (1979).

[b] Data from Berg and others (1998)

[c] Data from Opperman (2005)

It may be possible for private landowners in the upper Salinas River watershed to increase the volume of dead fallen hardwood LW in streams on their properties through the use of best management practices (BMPs) as suggested in Opperman and others (2006). Such practices have not yet been determined or tested for this region, but would likely include activities to: (1) promote the regeneration of hardwood riparian trees such as oaks, California sycamore, Fremont cottonwood, and willows; (2) promote the survival of hardwood seedlings; (3) allow trees to reach a size at which their DBH would be sufficient to allow them to function as LW; and (4) leave fallen dead LW in the channel to contribute to fish habitat such as pools. The development of BMPs for LW would thus be a valuable step in riparian management and steelhead recovery, given the broad distribution of fish in the watershed, the concerns of landowners over fish-related regulations, and the role of hardwood LW in contributing to pool habitat. The adoption of voluntary BMPs should increase the capacity of private landowners, resource agency staff, and public interest groups to cooperate in the management of fish-bearing streams on hardwood-dominated lands.

Acknowledgments

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Continue

Restoration and Regeneration

Continue

Regeneration of California Oak Woodlands 2001-2005[1]

Tara Barrett[2] and Karen Waddell[3]

Abstract

The first (1981-1984) and second (1991-1994) statewide inventories of California's oak woodlands found low levels of regeneration for several common oak species. In 2001, a new statewide inventory of California's oak woodlands was initiated, with 10 percent of field plots measured each year. The first five years of data (2001-2005) were used to examine regeneration and sapling distributions in common oak woodland types. Blue oak (*Quercus douglasii* Hook. & Arn.), valley oak (*Quercus lobata* Nee), and coast live oak (*Quercus agrifolia* Nee) forest types are characterized by low numbers of saplings, having mean levels of 60.5 (+/- 10.2), 22.2 (+/-9.8), and 77.8 (+/- 18.7) trees per acre for all species of trees in the 1 to 5 inches diameter breast height (DBH) class. In this third decade of monitoring, diameter distributions for blue oak and valley oak departed from the expected inverse-J shape. Better information on population-wide growth and mortality of saplings would be useful for understanding whether these observations indicate trouble ahead for the long-term sustainability of these oak species.

Keywords: California oak, forest monitoring, oak savannah, oak woodland, recruitment.

Introduction

The sustainability of oak woodlands is a matter of concern in California, due to issues such as conversion of forest to developed land (Bolsinger 1988), the introduction of *Phytophthora ramorum* and its effect on California black oak and coast live oak (Rizzo and others 2002), and low levels of regeneration and sapling recruitment for the more xeric oak forest types (Tyler and others 2002).

The low level of observable recruitment for some oak species has been commented on over the decades (Sudworth 1908), although there is considerable debate about whether it is truly a problem for long-term viability of oak woodlands (Tyler and others 2006). Explanations for low levels of recruitment include consumption by wildlife, livestock, and insects; environmental and chemical inhibition from introduced grasses, and other environmental factors (McDonald 1990). While blue oak has been the focus of the bulk of research on regeneration, other species including valley oak, coast live oak, and Oregon white oak (*Quercus garryana* Hook.) have also been studied.

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[1] An abbreviated version of this paper was presented at the Sixth California Oak Symposium: Today's Challenges, Tomorrow's Opportunities, October 9-12, 2006, Rohnert Park, California.

[2] Research Forester, Forest Inventory and Analysis, Pacific Northwest and Southwest Research Stations, Anchorage Forestry Sciences Lab, 3301 C Street Suite 200, Anchorage, AK 99503. e-mail: tbarrett@fs.fed.us.

[3] Analyst, Forest Inventory and Analysis, Pacific Northwest and Southwest Research Stations, P.O. Box 3890, Portland, OR 97208. e-mail: kwaddell@fs.fed.us.

It is impractical to monitor statewide sustainability of oak populations using age information, as seedlings and saplings are not bored due to concerns about harming the trees. Tyler and others (2006) suggest that the size structure of oak populations can serve as a method for monitoring sustainability, despite the only moderate correlation between size and age in oak populations. Diameter at breast height (DBH) measurements have been the most frequently used size-class method for monitoring tree populations. Numbers of trees by diameter class are used here as a direct metric for monitoring oak species.

Assessing whether regeneration of oak woodlands is sufficient for sustainability would require knowing rates of regeneration, growth, and mortality. With a diameter class model for sustainability, these rates would be expressed in terms of numbers of trees entering and leaving specific diameter classes within specific time periods. A simple diameter class population model for a tree species can be written as:

$$[1] \quad \mathrm{N}_0 = \sum_{i=1}^{D\max} r_i \mathrm{N}_i$$

$$[2] \quad \mathrm{N}_i = \sum_{j=0}^{D\max} G_{ij} \mathrm{N}_j \; - m_i \mathrm{N}_i \quad \forall\, i = 1, .., \mathrm{D}_{\max}$$

$$[3] \quad \mathrm{N}_{\mathrm{Dmax}+1} = 0$$

where N_i is the number of trees in the diameter class i, $\mathrm{D}_{\max}$ is the maximum diameter class, r_i and m_i are the regeneration and mortality rates for diameter class i, and G is a vector of growth (or shrinkage) rates for transitions from each diameter class j into diameter class i. When growth (G), mortality (m), and regeneration (r) are constant over time, the distribution of the population over diameter classes would be expected to slowly approach equilibrium regardless of the initial starting distribution, or, if in the equilibrium distribution, would stay constant. For a given tree species, the shape of an equilibrium diameter distribution of the entire population takes the form of an inverted J-shaped curve. Species with low-regeneration and low-mortality rates can be expected to have characteristically different diameter distributions than species with high-regeneration and higher-mortality rates, but both will resemble an inverse J-shaped curve. Diameter distributions that shift over time can either indicate recent changes in mortality, growth or regeneration, or they can indicate a past change to which the population is continuing to adjust.

The first (1981-1984) statewide inventory of oak woodlands found low regeneration of some species (Bolsinger 1988), as did the second (1991-1994) inventory (Waddell and Barrett 2005). In this paper, we present initial results from the third (2001-2005) statewide inventory of oak woodlands in California, focusing on regeneration and sapling recruitment. Diameter class distributions are presented as a snapshot indicator of population-level dynamics.

Methods

Data were from the annual Forest Inventory and Analysis program, which inventories forestland in the United States (Gillespie 1999) through a combination of remote sensing data and field plots. All forestland in California—public and private—is monitored through this program, with one-tenth of all field plots measured each year beginning in 2001. For this project, we used the 2001-2005 data, consisting of 8,328 plots of which 2,754 were at least partially forested. Although these data represent only half of the plots scheduled to be installed in California, the sampling intensity is equivalent to that used for oak woodland in the 1991-1994 inventory and roughly twice the sampling intensity of the 1981-1984 inventory used by Bolsinger (1988) in the first oak woodlands report.

Other changes between the second and third inventories include a change to the procedure used to determine forestland, changes in the layout of the field plot, changes in the procedures used to classify forest types, and a change from variable radius to fixed radius tree selection. In addition, all forestland is included in 2001-2005 inventory, whereas the second inventory excluded reserved land such as state and national parks, and the first inventory excluded reserved land and national forest land.

Each field plot consists of four subplots, which are themselves composed of nested circles within which trees of various sizes are measured for DBH, height, species, and live crown ratio (USDA 2005). Trees larger than 24.0 inches DBH are measured within a 58.9-foot radius circle (a “macroplot”), trees 5.0 to 23.9 inches DBH are measured on a 24-foot radius circle (a “subplot”), and saplings less than 5.0 inches are measured on a 6.8-foot radius circle (a “microplot”). The total plot area on which forest conditions are mapped is 1 acre.

All data used here are available through the national FIA Web site (www.fia.fs.fed.us/) or by request at the regional FIA Web site (www.fs.fed.us/pnw/fia/). Diameter distributions, tree per acre estimates, and sampling error were calculated with standard methods (Bechtold and Patterson 2005). Forest types were calculated using a classification algorithm (Stanford and others 2001).

Results and Discussion

Relative to other forest types, blue oak and valley oak forest have sparse seedling occurrence (*fig*. 1). The metric used to measure relative abundance of seedlings is to count the number of microplots into which at least one seedling fell. Although this metric can be useful for comparing relative seedling abundance between forest types, or for monitoring relative seedling abundance over time, sparse seedling occurrence does not necessarily indicate seedling occurrence that is below replacement level.

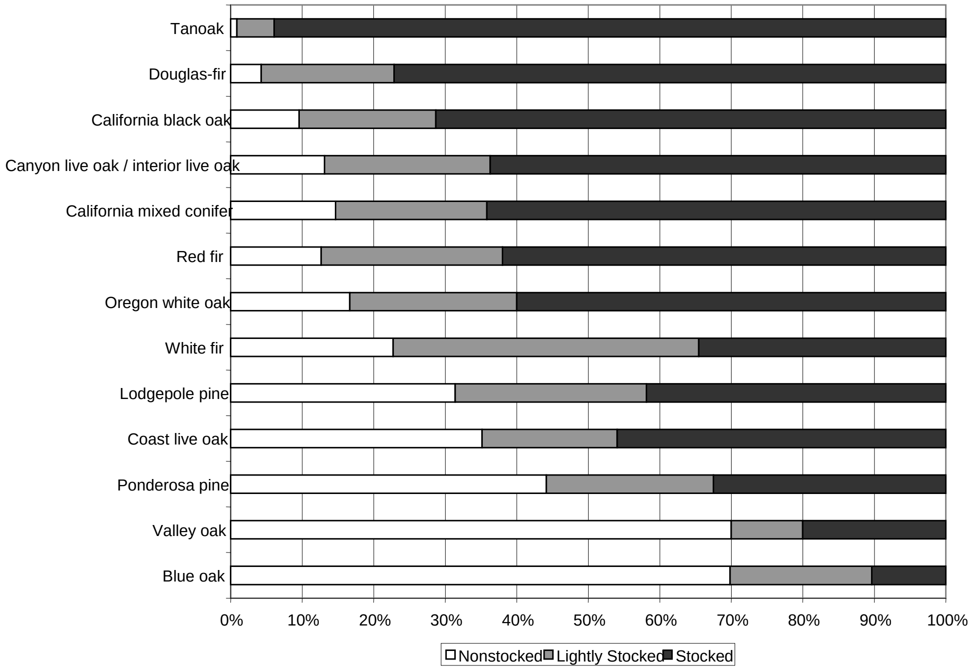

Figure 1—Percent of FIA plots 2001-2005 by seedling stocking class. Includes seedlings of all species within plots of homogenous forest type. Nonstocked = 0 of 4 microplots with seedlings; Lightly stocked = 1 of 4 microplots with seedlings; Stocked = 2 or more microplots with seedlings.

For the 2001-2005 inventory, the diameter distributions of interior live oak (*Quercus wislizeni* A.DC.) and California black oak (*Quercus kelloggii* Newb.) both resemble the classic inverse-J shape (*fig. 2*). California black oak's distribution differs from interior live oak's distribution as would be expected of a species with relatively lower rates of regeneration and mortality.

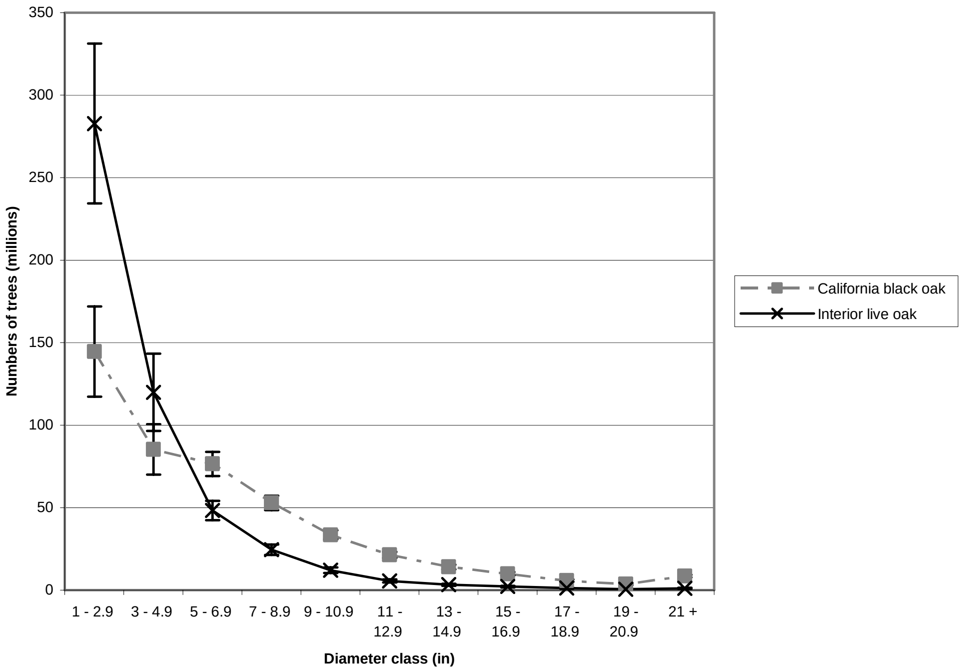

Figure 2—Diameter class distribution for California black oak and interior live oak, all California forestland 2001-2005.

The common oak species that are found in more open xeric conditions have a greater departure from typical diameter distributions (*fig. 3*). The distribution curve for Oregon white oak most closely resembles typical tree species, while blue oak, coast live oak, and valley oak all show convexity over part of their distribution. Some of this may be explainable by sampling error, which is particularly high for trees less than 5 inches diameter at breast height (DBH) because these trees are only measured on the very small (6.8-foot radius) microplots.

There are several reasons why convexity in a diameter class distribution could occur. Even with constant regeneration and mortality rates, variations in growth rates could explain this. When mortality rates are very low, a slower growth rate in a larger diameter class can result in convexity, as individual trees are in the small diameter class for a shorter period of time. In addition to diameter growth changes caused by aging, sapling growth can be increased by short-term environmental changes such as higher levels of precipitation or seasonal changes in the distribution of rainfall (Hanson and others 2001).

Convexity could be caused by mortality rates that are higher for certain diameter classes for a specific interval of time. For example, a decade with larger areas of forest burned, if the fires cause higher mortality in smaller diameter classes, could create convexity in the population distribution. These types of causes would be most likely to occur for species that have small geographic ranges, as the probability of a large percent of the population being affected by a stochastic event is higher.

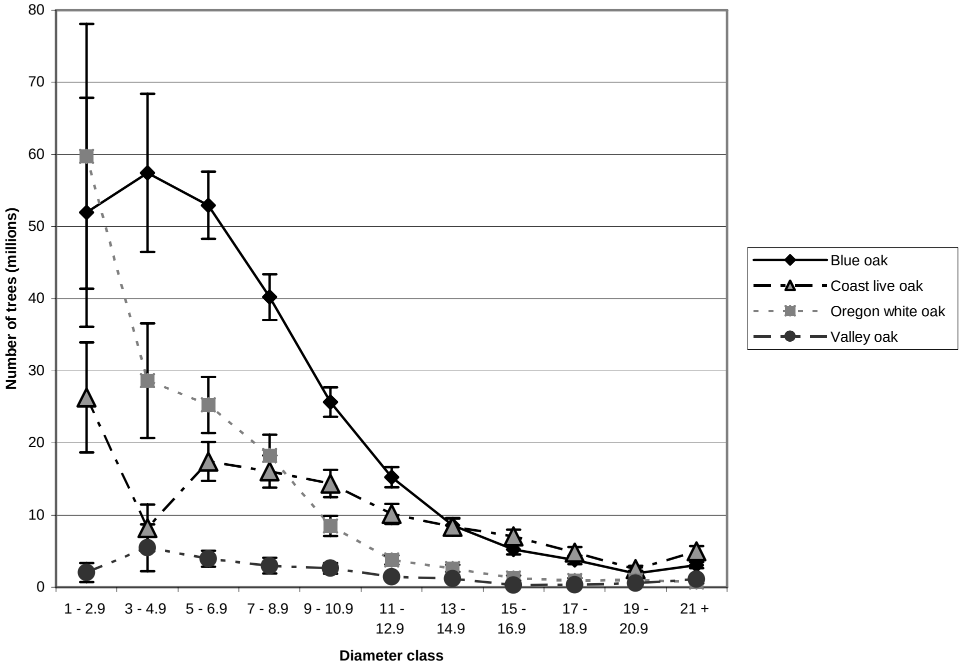

Figure 3—Diameter distributions for blue oak, coast live oak, Oregon white oak and valley oak, all California forestland, 2001-2005.

A third explanation for convexity in a diameter distribution is regeneration rates that have decreased over time. One method to help understand whether changes in rates of regeneration and mortality are affecting the population is to track the diameter distribution over time. Looking at diameter distributions of blue oak for three successive inventories is not conclusive, but it appears that changes in regeneration or mortality for small saplings may have occurred in the past (*fig. 4*).

Even when the ratio of large trees to small trees is high, mortality and growth rates are needed to understand sustainability. For example, in the 2001-2005 inventory, the ratio of number of blue oak trees in the 1- to 3-inch DBH class to the number of blue oak trees in the 11- to 13-inch DBH class is 3.4:1. Past FIA inventories provide some growth information that can be used to aid understanding of the sustainability of this ratio. Average diameter growth for blue oak saplings between 1981 and 1984 and 1991 and 1994 was 0.53 inches per decade for 1- to 3-inch DBH trees, 0.61 inches per decade for 3- to 5-inch DBH trees, 0.60 inches per decade for 5- to 7-inch DBH trees, 0.68 inches per decade for 7- to 9-inch DBH trees, and 0.70 inches per decade for 9- to 11-inch DBH trees (n=37; 41; 39; 34; 37). Assuming a 0.70 inch/decade growth rate, an individual tree might take 140 years to grow from 2 inches DBH to 12 inches DBH. With the assumption of 140 years for growth, the annual survival rate for 2-inch DBH trees growing to 12 inches DBH trees would have to be 99.1 percent to sustain the 3.4:1 diameter class ratio that was observed in the 2001-2005 inventory.

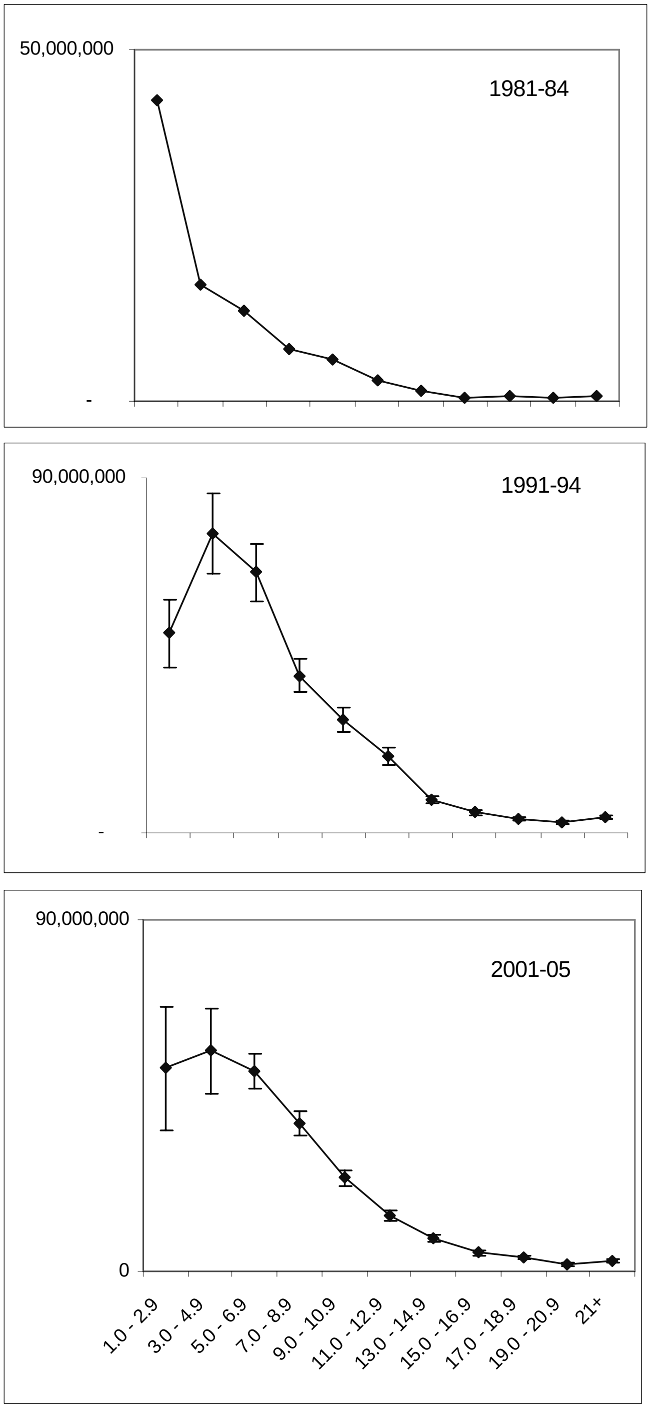

Figure 4—Diameter distributions of blue oak from three successive forest inventories of California. Absolute numbers are not comparable because of differences in the included land base.

Overall, saplings are sparse in blue oak, coast live oak, and valley oak forest types (*table 1*). These three oak forest types, with corresponding species that depart furthest from the classic inverse-J diameter distribution, also have the lowest overall density, measured in trees per acre (*table 1*). With open stand structures (few trees of any size) even moderate changes in regeneration can have long-lasting effects on the size distribution of the population. Although a low-mortality rate should contribute to the stability of a population, a tree species that is characterized by slow growth, slow regeneration, and a low-background mortality rate also has less potential to recover from disturbances. Because blue oak and valley oak are endemic to California, and coast live oak is endemic with the exception of a few small areas in Mexico, low regeneration observed from this statewide monitoring could indicate problems with sustainability for these three species.

Table 1—*Number of trees per acre on oak woodland forest types in California, 2001 to 2005.*[1]

	Diameter class (in)					
	1 – 4.9	5 – 9.9	10 – 14.9	15 – 19.9	20+	All classes
Forest type	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)
Blue oak	60.5 (10.2)	49.2 (2.6)	15.9 (0.9)	5.2 (0.5)	2.3 (0.2)	133.1 (11.1)
Canyon live – interior live oak	345.2 (27.8)	109.7 (5.4)	26.3 (1.5)	7.4 (0.6)	4.6 (0.4)	493.1 (28.3)
Coast live oak	77.8 (18.7)	58.5 (5.1)	28.4 (2.8)	14.7 (1.4)	7.2 (0.8)	186.5 (20.2)
California black oak	242.7 (31.4)	90.2 (7.2)	29.6 (2.1)	10.5 (1.0)	6.5 (0.6)	379.5 (33.8)
Valley oak	22.2 (9.8)	45.8 (10.3)	13.0 (3.1)	2.3 (0.7)	4.8 (1.3)	88.0 (15.2)
Oregon white oak	227.8 (35.2)	91.9 (8.7)	24.0 (2.3)	7.2 (1.2)	2.8 (0.7)	353.7 (36.4)

[1] Includes trees of all species

Conclusion

Based on the 2001-2005 inventory, sapling recruitment of blue oak, valley oak, and coast live oak appears to be low for the statewide population. These species show diameter distributions that are atypical for forest tree species, but these species are also atypical in their very open low-density woodland structure. Sparse regeneration and low density of small saplings for blue oak has been consistently observed for three decades of forest inventory, and in observational records for nearly a century. Diameter distributions are useful in understanding the populations' structures, but it is not possible to know whether the lack of regeneration results in non-sustainable populations from diameter distributions alone. Better information on statewide regeneration (r_i), growth (G_{ij}), and mortality rates (m_i) would allow dynamic modeling of the population structure and enhanced ability to monitor for long-term sustainability for these species.

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Stump Sprouting of Blue Oaks 19 Years After Harvest[1]

Doug McCreary,[2] Bill Tietje,[2] and Bill Frost[3]

Abstract

In 1987, a study was initiated to determine how the sprouting of harvested blue oak (*Quercus douglasii*) trees was affected by the season the trees were cut down, the height of the residual stumps, and whether the stumps were protected by fencing. Five sites throughout the range of this species were selected, and at each site 192 trees were harvested. After 19 years, 31 percent of the stumps had viable sprouts. The greatest differences among treatments were between stumps protected with fencing and those unprotected from browsing animals, with five times as many protected stumps surviving, compared to unprotected ones. Twice as many 90-cm-tall stumps than basal-cut stumps had surviving sprouts, 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 response variables. However, there were no clear site attributes to explain these differences. These results indicate that if the cutting of trees in densely stocked blue oak stands is necessary, it may be possible to alter stand age structure and promote 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 natural regeneration.

Keywords: Browsing, Quercus douglasii*, regeneration, stumps, thinning.*

Introduction

Purpose of Original Study

For nearly a century there has been concern that several native California oak species are not regenerating adequately to sustain populations (Jepson 1910). One of the species identified as having poor regeneration is blue oak (*Quercus douglasii*), a member of the white oak sub-genera endemic to the state (Bolsinger 1988, Muick and Bartolome 1987, Swiecki and others 1997). This species has a wide distribution, extending from the Siskiyous in the north to the Tehachapis in the south. It is commonly described as forming a "bathtub ring" around the Central Valley, with extensive stands along the lower elevation foothills of the east side of the coast range, the west side of the Sierra Nevada, and the foothills of the transverse ranges.

Because natural regeneration of blue oak is not always adequate to replace mortality (Bolsinger 1988, Muick and Bartolome 1987, Swiecki and others 1997), we wanted to determine whether sprouting could successfully help reestablish a new cohort of trees in cases where trees were going to be harvested to meet other management objectives (firewood harvesting, thinning densely stocked stands, etc.). If it could, then tree harvesting might result in multi-aged stands, partially mitigating concerns about poor natural regeneration and helping to promote stand longevity.

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[1] An abbreviated version of the paper was presented at the Sixth California Oak Symposium: Today's Challenges, Tomorrow's Opportunities. October 9-12, 2006, Rohnert Park, California

[2] Natural Resources Specialists, University of California Cooperative Extension (UCCE).

[3] [3] Natural Resources Advisor, University of California Cooperative Extension (UCCE.).

One of the principal objectives of this project was therefore to identify variables that influence sprouting. The variables examined in this study were stand location, season of harvest, stump height, and protection of the sprouts from browsing animals.

Methods of the Original Study

In 1987, we identified five densely stocked blue oak stands throughout its range in California to determine sprouting response in a wide range of environments. The stand characteristics at each of these sites are shown in *table 1*. The five 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 foothills of the Sierra Nevada. Four plots were established at each site. Each of these plots 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. Two plots per site 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 and eliminating browsing of any new sprouts that emerged following harvest. While the unfenced plots at all sites were grazed by domestic livestock, season of use and stocking rate were not recorded.

***Table 1**—Site characteristics of the blue oak harvest sites*[1]

Site	Density (stems/ha)	Basal area (m2/ha)	Average DBH (cm)	Annual precip. (cm)	Soil depth (cm)	Soil texture
Mendocino	483	19	19.8	93	60	Silt loam
Glenn	518	9	13.7	55	70	Clay loam
Butte	464	15	18.5	52	45	Clay loam
Amador	470	12	15.0	46	100	Grav. loam
San Luis Obispo	485	11	14.7	55	42	Grav. loam

[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.

Within each plot, all trees were tagged with sequential numbers from 1 to 96. Half of the trees within each plot were randomly selected for harvest. Of these 48 harvest trees per plot, 12 were chosen randomly for harvest in each of the four seasons (summer, fall, winter and spring). Half of the 48 trees were selected to be cut 90 cm above the ground and half for cutting at the base of the tree.

All plots were evaluated in 1988, 1989, 1997, and 2006. Each harvested stump was evaluated for presence or absence of living sprouts, number of sprouts, and length of the tallest sprout. During the last two evaluation dates, the diameter of the largest living sprout per stump was also recorded. Prior to the 2006 assessments, sprouts were also assessed for browsing damage.

Results from the earlier evaluations for this study were presented in 1990 at Symposium on Oak Woodlands and Hardwood Rangeland Management at Davis in 1990 (McCreary and others 1991), and in 2001 at the Fifth Symposium on Oak Woodlands (McCreary and others 2002). The 1990 results indicated that harvest date had relatively little influence on sprouting, while stump height had a large effect, with a far 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 lengths. Incidence of sprouting was negatively correlated with DBH.

In the 2002 paper, we reported that site and stump height still had significant impacts on sprouting response 10 years after harvest. However, unlike the evaluations in 1988 and 1989, protection of the sprouts was the most influential variable with nearly four times as many protected stumps having living sprouts (54 percent) as unprotected stumps (14 percent).

Methods of the 2006 Evaluation

In summer 2006, all plots were revisited and all stumps that had living sprouts were measured. After 19 years, not all the original stumps that failed to sprout or whose sprouts had died could be located, due to decay and deterioration. We are confident we located all stumps with living sprouts because they were easy to see and find, especially with the assistance of plot maps that showed the location of all of the original stumps. Each stump with living sprouts was assessed for the number of sprouts emerging from the stump, the length of the longest living sprout, and the diameter of the largest living 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 sprout clump. Except for sprout diameter, these same variables had also been recorded during each of the three previous assessments.

As it was for the earlier assessments, data was analyzed 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 sprout mortality, by 2006 (as well as for the 1997 data) a simplified model was required to analyze all variables. Because few differences were found for harvest dates when this study was evaluated in earlier assessments, the simplified model we used combined responses among harvest dates.

Results

Survival (the percentage of stumps with living sprouts)

Although sprout survival increased slightly during the first two years of the study (*table 2*), between 1989 and 1997 it dropped markedly. Between 1997 and 2006 there was a continued reduction in survival, but at a far diminished rate. Average survival for the entire study dropped from 34 percent at time of the last assessment in 1997, to 31 percent in 2006 (*table 2)*. The greatest reduction in survival occurred at the San Luis Obispo site, dropping from 38 percent in 1997 to 32 percent in 2006.

However, the reduction in survival for all sites combined was not equally apportioned among treatments, with the largest reduction in survival for stumps in unfenced plots. In 1989, average survival of unfenced stumps was 59 percent. By the 1997 assessment, this had dropped to 14 percent. By 2006 it had gone down further, to 11 percent, a reduction of more than one-fifth (*table 4*). In contrast, average survival of fenced stumps was 67 percent in 1989, 54 percent eight years later, and 51 percent in 2006. There were also significant differences between the survival of basal stumps and those cut at 90-cm, with the taller stumps having more than twice the average survival of those cut at ground level (42 percent vs. 20 percent) (*table* 5). This was consistent with results from measurements taken nine years earlier.

Table 2*—Average survival (percent) for the five sites for each of the 4 measurement periods* [1].

Site	**1988**	**1989**	**1997**	**2006**
Mendocino	62 a	72 a	29 a	26 a
Glenn	34 b	37 b	28 a	28 a
Butte	63 a	65 a	44 a	40 a
Amador	59 a	65 a	32 a	29 a
San Luis Obispo	73 a	76 a	38 a	32 a
Total	58	63	34	31

[1] Values within a column are significantly different ($P< 0.05$) if they are followed by a different letter (Fisher's protected LSD test).

Table 3*—Average response of different sites 19 years after harvest* [1].

Site	**Sprout survival (%)**	**Number of sprouts**	**Sprout length (m)**	**Sprout diameter (cm)**
Mendocino	26 a	15.0 a	1.9 a	2.8 a
Glenn	28 a	7.8 b	2.3 ab	4.6 ab
Butte	40 a	3.0 c	4.1 c	7.7 c
Amador	29 a	3.9 c	3.4 bc	6.7 bc
San Luis Obispo	32 a	8.2 b	2.7 ab	3.8 ab

[1] Values within a column are significantly different ($P< 0.05$) if they are followed by a different letter (Fisher's protected LSD test).

Table 4*—Average response of different fencing treatments 19 years after harvest* [1].

Fencing Treatment	**Sprout survival (%)**	**Number of sprouts**	**Sprout length (m)**	**Sprout diameter (cm)**
Unfenced	11 a	9.5 a	2.1 a	3.7 a
Fenced	51 b	5.7 b	3.6 b	6.5 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).

***Table 5** —Average responses of different stump heights 19 years after harvest [1].*

Stump height	Sprout survival (%)	Number of sprouts	Sprout length (m)	Sprout diameter (cm)
Basal	20 a	6.1 a	2.3 a	4.4 a
90 cm	42 b	9.1 b	3.5 b	5.8 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).

Number of Sprouts

The average number of living sprouts per living stump declined steadily over time, a trend that continued into 2006. The average number of sprouts per living stump was 30.6 in 1989, 8.4 in 1997, and 7.6 in 2006. There were significantly more sprouts per stump in unfenced plots (*table 4*), and taller stumps had significantly more sprouts than basal stumps (*table 5*). There was also a significantly larger number of sprouts on stumps at the Mendocino site than at the other four sites (*table 3*).

Sprout Length

The lengths of the longest sprouts were significantly greater in fenced than in unfenced plots (*table 4*); lengths were also greater for taller stumps (*table 5*). There were significant differences in sprout length among harvest sites, with those in Mendocino being significantly shorter than those in Butte or Amador counties (*table 3*).

Sprout Diameter

Sprout diameter and sprout length followed a similar pattern. There were significantly larger diameter sprouts for taller stumps (*table 5*) and for stumps within fenced areas (*table 4*). As was the case for sprout length, sprouts in Mendocino were significantly thinner than those in Butte or Amador counties (*table 3*).

Interactions

There were several interactions among response variables that warrant comment. For survival, there was a significant interaction between fencing and stump height. Even though the taller stumps had greater survival in both fenced and unfenced plots, the magnitude of the difference was much greater in the fenced plots.

There were also significant interactions for height and diameter. For height, there was a significant interaction between site and stump height and between site and fencing treatment. At all sites, taller stumps grew more than shorter stumps and fenced stumps grew more than unfenced stumps. However the magnitude of these differences varied considerably among sites, ranging from only being slightly greater, to being more than double (the heights were more than twice as tall).

The interactions for diameter followed a similar pattern. At all sites except one (Glenn), shorter stumps had smaller diameters than taller stumps. At the Glenn site, however, the shorter stumps had slightly larger average diameters, though these differences were not significant. At all sites except one (Amador), fenced stumps had larger diameters than unfenced stumps. At this site, however, the diameters of stumps in fenced plots and unfenced plots were very similar, but were slightly larger—though not significantly so—in unfenced plots.

Finally, there was also a significant interaction between fencing and stump height for diameter. Taller stumps had greater diameters both within and outside fences, but these differences were greater in the unfenced plots.

All in all, the significant interactions indicate that the responses to stump height and fencing at the different sites were quite similar—with taller stumps and fenced stumps performing better than shorter or unfenced stumps—but that the degree of difference between these treatments can and does vary somewhat by site.

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 stumps after the top of the tree was killed by fire or felling. For example, studies reveal that harvested stands or stands destroyed by fire were replaced by multiple-stem trees of similar age, presumably from sprouting (McClaran and Bartolome 1989, Mensing 1992). Sprouting is apparently an adaptive strategy that allows trees to remain alive and reoccupy a site following disturbance.

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). In general, the smaller stumps tended to sprout more, 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.

One of the initial goals of this study was to identify variables that influence sprouting so that when harvesting is done as part of other management objectives, it may be possible to promote sprouting in the resultant stumps. Encouraging sprouting could then be used to promote stand longevity and even if natural regeneration was insufficient to replace mortality under natural circumstances, lengthening the life of stands could allow more time for seedling recruitment to occur. However, because there would be more ladder fuels, such stands may be more susceptible to catastrophic fire and they would remain vulnerable to anthropogenic pressures including development, agricultural conversions, and firewood harvesting. It is also worth mentioning that many blue oak stands are regenerating adequately and sprout regeneration would not be necessary or encouraged.

It was further speculated that opening the stands up through thinning, and fencing out grazing and browsing animals, might also promote natural regeneration, though these effects were not officially evaluated in the study. However, previous research has demonstrated that thinning of blue oaks can result in increased acorn production (Standiford and others 1999) that could lead to greater regeneration of seedlings. We also did observe many vigorous naturally regenerating oak seedlings in fenced plots, especially at the plot in Mendocino County. In contrast, few seedlings were observed in unfenced plots.

The data from this study suggest that sprouting can be used to alter age structure in stands since, after 19 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, especially protection from browsing animals using fencing. In most locations, nearly two decades of exposure to browsing animals resulted in high sprout mortality and greatly 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 the sprouts on all but one stump being killed in the unfenced plots. In addition to causing increased mortality at all sites, browsing in unfenced plots reduced sprout size, but tended to increase the number of sprouts per stump. Repeated browsing apparently caused the stumps to continue producing more young sprouts and interrupted the normal thinning response observed inside the fenced plots. The data also demonstrated that if the sprouts survive for a decade, there is a high likelihood they will remain alive for at least 19 years.

While there were differences in sprout growth among sites, it is not clear what site variables were likely responsible. 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 height and diameter growth (Butte and Amador) were at the two lowest elevations. It is also possible that stump diameter adversely affected sprout response since the stumps at the Mendocino site had the largest average diameters.

Another concern we had after the study was in place for only two years was that the tall stumps from which sprouts were growing might decay more rapidly, causing the sprouts to die. After 19 years there is no evidence that this is a serious problem, and fewer 90-cm stumps had sprout mortality between 1997 and 2006 than did basal-cut stumps. By 2006, the average percent sprouting for 90-cm stumps was more than double that for basal-cut stumps, and the average height and diameter of sprouts from taller stumps were significantly greater than for sprouts growing from basal-cut stumps. It thus appears that retaining taller stumps during harvest promotes greater sprouting success.

Finally, it should be mentioned that there are other potential drawbacks to relying exclusively on stump sprouting to regenerate harvested stands. While a substantial number of harvested trees in this study did sprout, we would expect the percentage to go down with each harvest cycle. That is, trees likely cannot be repeatedly cut down and continue to sprout. Also, sprout-origin trees are genetically identical to the harvested trees so there is no additional genetic diversity associated with sexual reproduction as there would be for acorn-produced trees. In forested stands where the environment is changing over time, as many predict from global climate change models, replacing trees from sprouting—rather than from acorns—may make it less likely that species will adapt to these changes.

Conclusions

Results from this study indicate that even after 19 years, over 30 percent of harvested trees have viable sprouts. Whereas there was considerable attrition in sprout survival between assessments in year 2 and year 10, sprout survival of all originally harvested trees only went down by 3 percent in the subsequent 9 years. The majority of stump death during this interval appeared to be caused by repeated browsing damage since 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.

Since the study was established in 1987, season of harvest has had relatively little impact on sprouting. However, 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. All in all, this study indicates that if blue oak stands are thinned for other management objectives, sprouting can help these stands replace themselves. Sprouting can alter stand structure and 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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Continue

Spatial Synchrony and Temporal Patterns in Acorn Production of California Black Oaks[1]

Barrett A. Garrison,[2] Walter D. Koenig,[3] and Johannes M.H. Knops[4]

Abstract

We studied spatial synchrony and temporal patterns of acorn production in California black oaks (*Quercus kelloggii*) at seven sites throughout California. At a small spatial scale, analysis of individuals in one site (Placer County) revealed highly significant spatial synchrony in annual acorn production for individuals up to 17.2 km apart, the maximum distance separating these trees. At the statewide scale, significant spatial synchrony was detectable among trees up to 814 km apart, again the maximum distance separating trees. Temporal patterns in annual acorn crops were negatively correlated with crops produced from two to five years before the current annual crop, consistent with the hypothesis that trees require multiple years to recover from masting events. The size of the mean annual acorn crop decreased while variation increased geographically with latitude. Although acorn crops were inconsistently correlated with environmental factors at individual sites, in general they were inversely correlated with total spring precipitation lagged one year, the time period corresponding with conditions during flower development and pollination. Total spring precipitation lagged one year increased with latitude in a pattern that mirrored the decline in acorn production. Our results indicate that the California black oak, a "two-year" species requiring two years to mature acorns, exhibits patterns of spatial and temporal synchrony in acorn production comparable to other "one-year" California oak species that have been analyzed to date.

Keywords: acorns, California, ecological variation, Fagaceae, *masting, oak,* Quercus kelloggii, *spatial patterns, spatial synchrony, temporal patterns.*

Introduction

Many species of North American oaks (*Quercus* spp.) produce annually variable acorns crops (Healy and others 1999, Koenig and Knops 2000, Koenig and others 1994a, Sork and others 1993). This variable pattern of acorn production is known as masting, a population phenomenon in which reproductive effort is temporally variable and spatially synchronized (Kelly 1994, Kelly and Sork 2002, Koenig and Knops 1997). These spatial and temporal elements must be demonstrated among populations and between individual plants within populations to demonstrate masting (Kelly 1994). Spatial synchrony, if it exists, may occur over large or small geographic areas, and is relevant to the evolutionary basis for masting (Koenig and others 1999). Temporal autocorrelations are similarly important insofar as they

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[2] Staff Environmental Scientist, Sacramento Valley-Central Sierra Region, California Department of Fish and Game, 1701 Nimbus Road, Rancho Cordova, CA 95670 (posthumously printed).

[3] Research Zoologist, Hastings Reservation and Museum of Vertebrate Zoology, University of California Berkeley, 38601 E. Carmel Valley Road, Carmel Valley, CA 93924. e-mail: koenigwd@berkeley.edu.

[4] Associate Professor, Department of Biological Sciences, University of Nebraska-Lincoln, 348 Manter Hall, Lincoln, NE 68588-0118. e-mail: jknops2@unl.edu.

provide evidence for resource shifting or differential resource allocation on the part of individual trees. Masting patterns by forest and woodland trees are of importance at the ecosystem level because mast is an important food of wildlife and is often an important source of plant recruitment (Kelly and Sork 2002, Koenig and Knops 2000).

California black oak (*Quercus kelloggii*) is the dominant oak in montane hardwood and coniferous forest habitats in California. The range of this species extends from south-central Oregon extensively throughout most of California's mountains, except for scattered populations in the mountains of the central coast ranges and the mountains of Southern California. There is also a small disjunct population in Baja California (McDonald 1990). Acorns are the source of sexual recruitment of California black oak, although asexual recruitment in the form of stump sprouting also occurs (McDonald 1990). Dozens of bird and mammal species feed on this tree's acorns, breed and rest in its cavities, and feed on the tree's flowers, foliage, and insects (Barrett 1980, Verner 1980). Acorns, however, are the most conspicuous of these resources used by wildlife, and thus patterns of acorn production are of particular interest to both evolutionary biologists and natural resource managers.

Previous studies have demonstrated that California black oak acorn production has considerable temporal and spatial variation, but these works have failed to reveal evidence of spatial synchrony (Koenig and Knops 1997, Koenig and others 1999). Here we extend these prior studies by testing for spatial synchrony and temporal autocorrelations in acorn production by this species over a much larger area and longer time span than previous studies and by including results from a study of a large number of trees within the main range of this species in the Sierra Nevada. In addition, correlations were calculated between mean annual acorn crops for the study populations and several weather variables to assess the potential environmental cues that may be used to generate the observed patterns of spatial synchrony. As suggested by Herrera and others (1998), most of our analyses focus on seed production by individual trees rather than population-level estimates of productivity.

Study Area and Methods

Acorns of California black oak were visually surveyed each year between 1994 and 2005 at seven sites in California (*fig. 1, table 1*). Spatial analyses were performed at two scales. At the "macrogeographic" scale (macro-scale), we included data from six populations that are part of a more geographically extensive study of long-term mast production by California oaks (Koenig and Knops 1997). With each of these populations, 20 to 25 trees were individually marked and acorns were annually counted in September. Within each site, trees were arbitrarily chosen, most being relatively large individuals presumably capable of producing larger and more frequent mast crops (*table 1*). Trees were scanned with binoculars, and viable acorns visible to observers were counted in two 15-second count periods and totaled to yield the total number of acorns counted in 30 seconds (Koenig and others 1994b). The six macro-scale populations were located throughout California and included trees up to 814 km apart spread over 7° latitude and 6° longitude and ranging in elevation from 370 to 1,500 m (*table 1*).

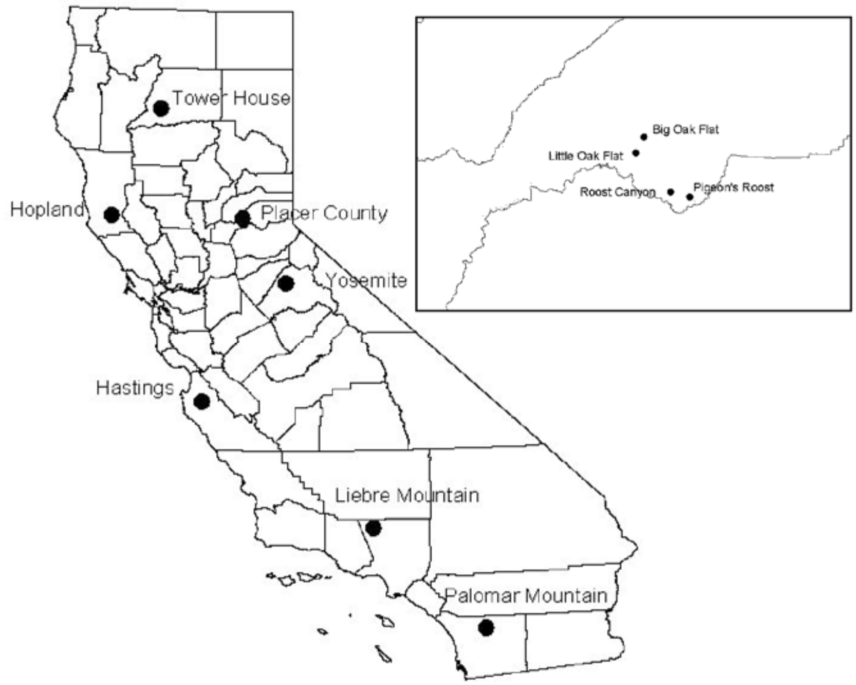


Figure 1—Sites used for study of acorn production in California black oaks at macro-scales and micro-scales. The inset shows the locations of the four micro-scale sites in Placer County.

At the "microgeographic" scale (micro-scale), we analyzed trees from four forest stands in Placer County (Garrison and others 1998). These populations included trees up to 17 km apart over approximately 10' latitude and 12' longitude and ranging in elevation from 1,190 to 1,340 m (*table 1*). The stands were chosen for a larger study of the effects of logging on wildlife (Garrison and others 2005a, 2005b). Within each of these four populations, acorns were counted on 142 to 144 tagged trees between mid-August to late-September. Acorns were counted in two 15-second count periods by a single observer and added to calculate the total number of acorns counted in 30 seconds. Sample trees were ≥ 25 cm dbh on 50-m spacing closest to the intersection points of a 25-m transect grid over two 6.25-ha study areas per stand. In addition, one smaller tree 13 to 25 cm dbh was selected at random from each of 11 longitudinal transects that made up the grid to measure acorn production of smaller trees. In all, acorn production data were analyzed from 702 individual trees. Counting methods used at all sites closely matched acorn counts using other methods such as traps and production categories (Koenig and others 1994b, Garrison and others 1998).

Table 1—*Characteristics of California black oak trees in populations used for study of synchrony in acorn production.*

Population	Elevation (m)	Latitude-Longitude	Tree diameters (cm) Mean ± SE (n) (range)
Macro-scale			
Palomar Mountain	1,500	33°20’ - 116°55’	80.9 ± 5.5 (20) (46.5-142.1)
Liebre Mountain	1,230	34°44’ - 118°41’	79.5 ± 7.1 (20) (41.5-148.5)
Hastings	790	36°12’ - 121°33’	82.0 ± 7.7 (21) (21.0-147.0)
Yosemite	1,200	37°45’ - 119°45’	84.5 ± 6.9 (25) (32.3-157.2)
Hopland	680	38°58’ - 123°07’	40.7 ± 2.6 (22) (21.5- 68.5)
Tower House	370	40°38’ - 122°34’	53.1 ± 3.9 (20) (24.2- 85.4)
Micro-scale			
Pigeon’s Roost	1,230	38°93’ - 120°55’	44.6 ± 2.0 (144) (14.5-147.6)
Roost Canyon	1,340	38°94’ - 120°58’	55.0 ± 2.2 (142) (14.5-134.2)
Little Oak Flat	1,290	39°04’ - 120°67’	51.2 ± 2.3 (142) (13.0-152.0)
Big Oak Flat	1,280	39°06’ - 120°66’	60.4 ± 2.4 (144) (13.2-137.2)

Acorn counts for each tree were log-transformed [log(x + 1)] for analysis. Because of differences in how trees were initially chosen in the two studies, there were considerable differences in size and other characteristics between the two data sets (*table 1*). Consequently, spatial synchrony was examined on the two non-overlapping geographic scales (micro- and macro-) using the data from trees within the Placer County site for the micro-scale analysis (dividing trees into < 5 km and 5 to 17 km distance categories), and trees from the remaining sites for the macro-scale analysis (dividing trees into 25 to 100 km, 100 to 250 km, 250 to 500 km, and 500 to 814 km distance categories). Statistical tests were performed using the modified correlogram technique of Koenig and Knops (1998). With this method, Pearson correlation coefficients (*r*) were calculated for annual acorn crops from all pairwise combinations of trees within the micro- and macro-scale groups with common annual data. Distances between trees were based on UTM coordinates. Within each distance category, we tested whether *r* values were statistically greater than 0 by performing randomization trials in which sets of correlation coefficients were chosen from the entire pool such that individual trees were only used once. Once a complete set of correlations from the non-overlapping pairwise combinations of trees was chosen, we calculated the mean *r* value and counted the number of positive and negative correlation coefficients present in the data set. A total of 1,000 correlation trials was performed for each distance category. Means (± SE) were calculated from the set of mean *r* values generated by the randomization trails. We also performed Mantel tests within the micro- and macro-scale groups of trees, another randomization procedure that in this case measures whether spatial structure is present in the data. Assuming spatial structure is present, it is expected a priori that synchrony will decline with increasing distance (Liebhold and others 2004).

Temporal patterns were assessed using partial autocorrelations, which test for relationships at annual lag intervals controlling for autocorrelations at shorter lag intervals. Autocorrelation coefficients up to a maximum lag of seven years were calculated using acorn production data for individual trees and then averaged across all trees. As with the spatial analyses, temporal autocorrelations were calculated for the two datasets separately. All analyses included trees surveyed from 1994 to 2005 except for the Hastings site, for which data were available going back to 1980.

To look for potential environmental cues that might be used by trees to determine reproductive investment, Spearman rank correlations were calculated between weather data (unlagged and lagged one year) and the mean acorn crop size from each of the seven sites. Weather data for 1992 to 2005 were collected from various sources at or as near as possible to the actual sites themselves, usually weather stations that are part of the NOAA/NWS cooperative weather observer network. Weather attributes included measures of total precipitation (cm) and average, minimum, and maximum monthly temperature (°C). Weather attributes were correlated with acorn production from the same year (unlagged) and lagged by one and two years, depending on the variable, prior to the year of the acorn count for the seven sites. Weather variables used were those previously used by Koenig and others (1996) (12 variables) and Koenig and others (1999) (4 variables) for assessment of weather on acorn production by California oaks. Eight additional weather variables were included that we felt might be important during flower initiation and pollination: unlagged and lagged one year measures of total precipitation and average monthly temperature (average, minimum, and maximum) during the spring (March, April, and May). Results were considered statistically significant when $P < 0.05$.

Results

Annual Acorn Production Patterns

Mean acorn crops at the macro-scale populations were generally larger than within the micro-scale populations (*fig. 2*), most likely reflecting the larger and presumably older trees chosen at the macro-scale sites. Within the macro-scale populations, there was a trend for larger acorn crops with the southern populations and smaller crops with the northern populations (Spearman rank correlation using overall mean acorn production at each site vs. latitude; $r_s = -0.89$, $n = 6$, $P < 0.05$). This trend was identical when the micro-scale population was included ($r_s = -0.89$, $n = 7$, $P < 0.01$) (*fig. 3*). Coefficients of variation for each population based on the acorn crops of individual trees increased, although not significantly, from south to north with the macro-scale populations ($r_s = 0.83$, $n = 6$, $P = 0.10$), a trend that became significant when the micro-scale population was included ($r_s = 0.82$, $n = 7$, $P < 0.05$) (*fig. 4*).

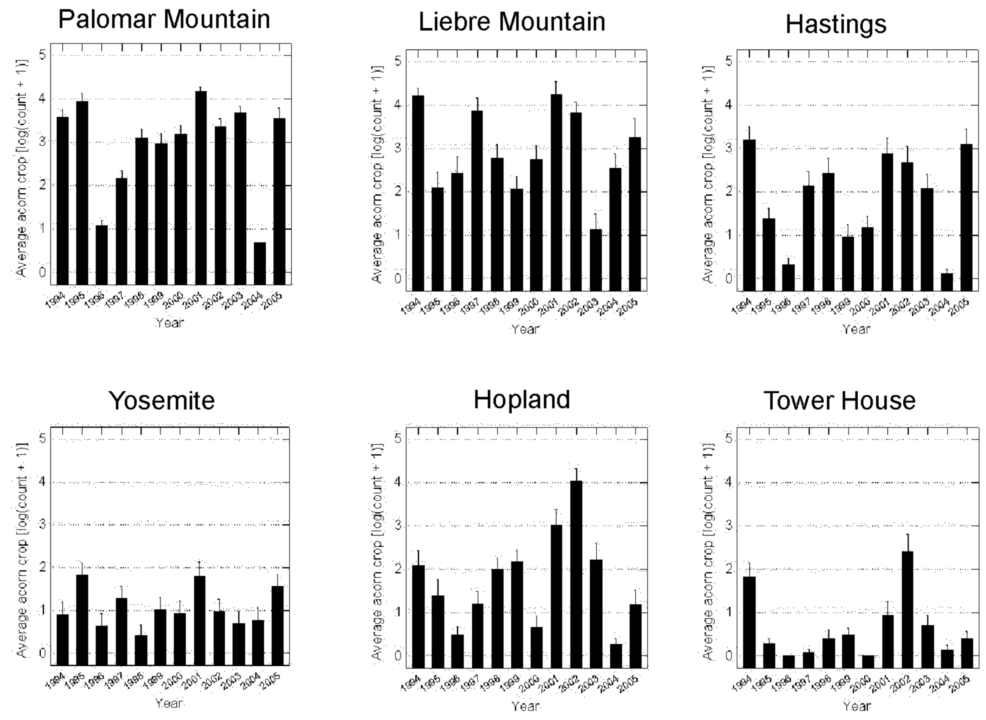
Spatial Synchrony

Spatial synchrony was generally higher at the macro-scale than the micro-scale, again presumably due to differences in the two sampling regimes. Consequently, data from the two studies could not be directly compared and were analyzed separately. Spatial synchrony was highly significant at the micro-scale level using the Placer County data and at the macro-scale level using the data from the other six sites (*table 2*). Despite the higher mean synchrony at the largest distance category (500 to 814 km) compared to the next smaller category in the macro-scale data, Mantel tests confirm that on average spatial synchrony declined with distance (micro-scale: Mantel $z = -0.068$, $P < 0.001$; macro-scale: Mantel $z = -0.176$, $P < 0.001$).

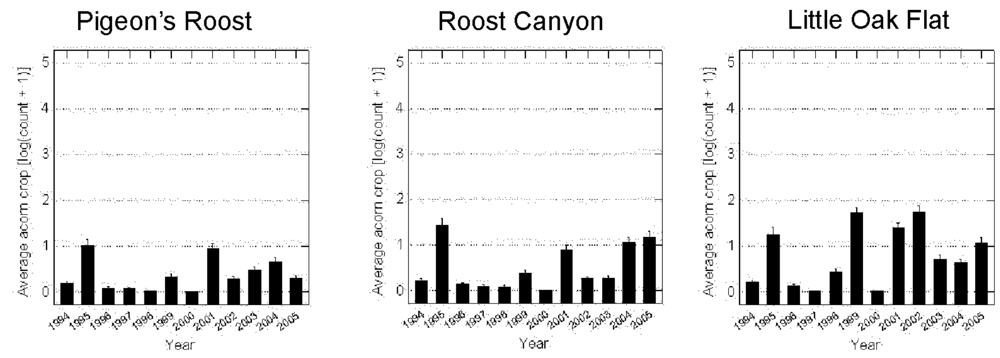
Temporal Patterns

Both datasets yielded strong and generally highly significant negative temporal autocorrelations at nearly all lags up to seven years (*fig. 5)*. Partial autocorrelations in trees used in the macro-scale analyses (*fig. 5*, bottom) exhibited a particularly strong negative autocorrelation at two-year intervals; that is, good acorn crops in year *x* were particularly likely to be followed by poor acorn crops two years later. Partial autocorrelations in the trees used in the micro-scale analyses (*fig. 5*, top) similarly had a strong negative value at lag 2 but were most strongly negative at lag 5, such that good acorn crops in year *x* were most likely to be followed by poor acorn crops five years later.

Macro-scale populations (*n* = 20 to 25 trees per population)



Micro-scale populations (n = 142 to 144 trees per population)



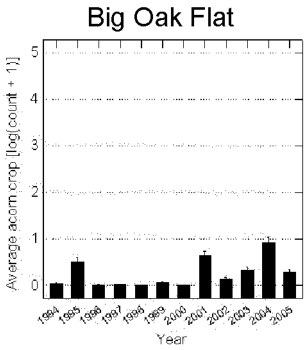


Figure 2—Mean ± SE of annual acorn crops (log-transformed) of California black oak between 1994 and 2005 from the six macro-scale populations, and the four populations used for the micro-scale analysis.

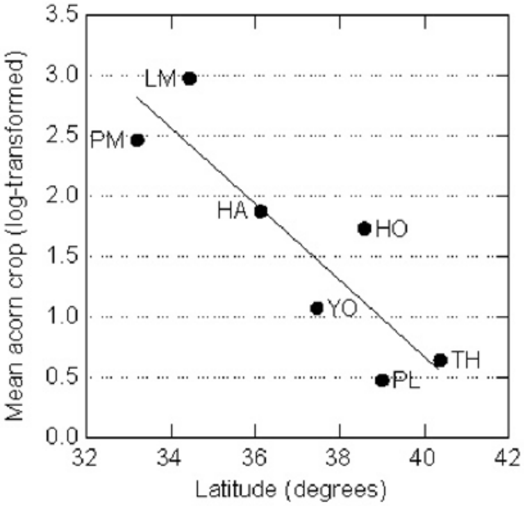


Figure 3—Relationship of latitude to mean annual acorn crops (log-transformed) for California black oak between 1994 and 2005 from seven populations in California. The line is a linear regression line of the means of the transformed values. Codes for the sites are: LM – Liebre Mountain; PM – Palomar Mountain; HA – Hastings; HO – Hopland; YO – Yosemite; TH – Tower House; and PL – Placer County.

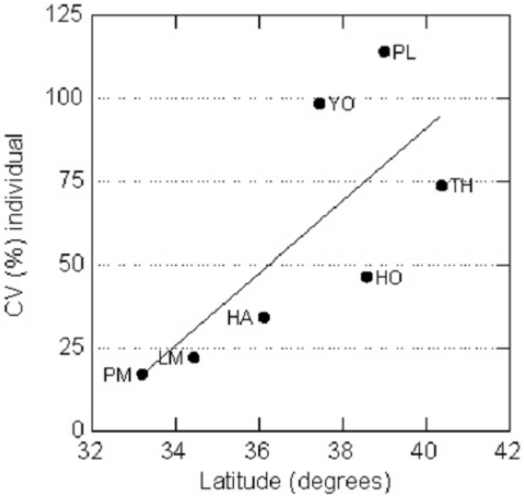


Figure 4—Relationship of latitude to coefficients of variation of annual acorn crops (log-transformed) for California black oak between 1994 and 2005 from seven populations in California. The line is a linear regression line of the means of the transformed values. See Figure 3 for codes.

Table 2—*Spatial synchrony in annual acorn crops of California black oaks. Values represent the mean (± SE) correlation between individual trees using the modified correlogram technique of Koenig and Knops (1998).*

Distance (km)	Mean *r*	SE	*P*-value
Micro-scale			
< 5 km	0.247	0.022	< 0.001
5 to 17 km	0.207	0.020	< 0.001
Macro-scale			
25 to 100 km	0.455	0.027	< 0.001
100 to 250 km	0.330	0.026	< 0.001
250 to 500 km	0.144	0.032	0.001
500 to 814 km	0.256	0.032	< 0.001

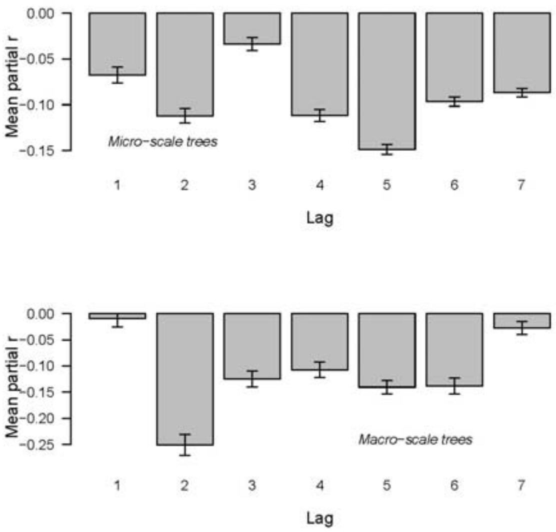


Figure 5—Partial autocorrelation coefficients for micro- (top) and macro-scale (bottom) trees for annual acorn crops lagged from 1 to 7 years. Values are means ± 1 SE.

Environmental Correlates of Acorn Production

Of the 168 individual Spearman correlation tests run for the seven sites, total spring precipitation and average spring temperature lagged one year had the strongest and most consistent relationships with mean acorn production (precipitation: average r_s = -0.34; temperature: average r_s = 0.35; both n = 7) among the seven sites (results of correlations on file, California Department of Fish and Game, Rancho Cordova, CA). However, only 14 of 168 (8.3 percent) pairwise correlations were significant (11 at $P < 0.05$; three at $P < 0.01$), two of which involved spring precipitation and average spring temperatures lagged one year at Hastings. Most (20 of 28 [71.4 percent]) of the spring and annual precipitation correlations with annual acorn crop were negative, while most (20 of 21 [95.2 percent]) acorn crop correlations with summer temperature lagged one year were positive. Correlations of unlagged summer temperatures with mean acorn crops were 57.1 percent (12 of 21) positive and 42.9 percent negative (9 of 21). Total spring precipitation and average spring temperature were highly negatively correlated (average r_s = -0.63; individual Spearman correlations at six of seven sites significant at $P < 0.05$; r_s = -0.59 to -0.87; n = 12).

Since these two weather variables were interrelated and hence redundant to some degree, total spring precipitation was averaged among all 12 years, along with annual acorn crops for the seven sites and then correlated to look for large-scale environmental factors affecting acorn production. Among the seven sites, average annual acorn crops decreased with increasing spring precipitation lagged one year (r_s = -0.89; n = 7; P = 0.01), and this relationship held for the six macro-scale sites in which the methods were most similar (r_s = -0.89; n = 6; P = 0.025) (*fig. 6*).

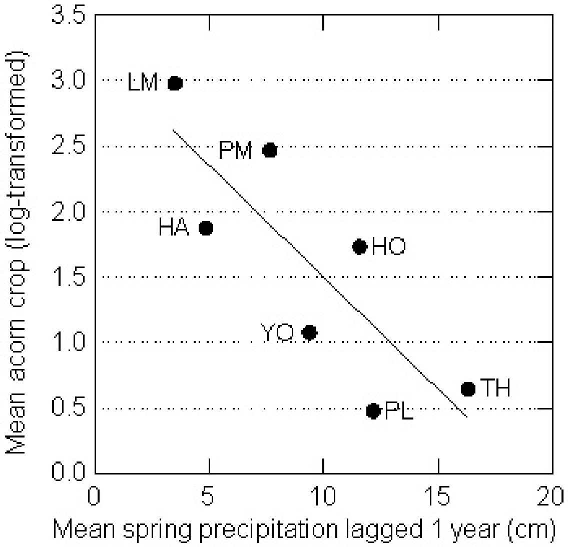


Figure 6—Relationship between mean annual acorn crops (log-transformed) of California black oak with mean spring precipitation lagged one year from seven sites in California between 1994 and 2005. The line is from a linear regression line of the means of the transformed values. See Figure 3 for codes.

Discussion

Of California tree oaks, California black oak is one of the most variable and unpredictable producers of annual acorn crops (Koenig and others 1994a, 1999). Previously, Koenig and others (1999) failed to demonstrate synchrony between two populations of California black oak 320 km apart in coastal California, and Koenig and Knops (1997) could not demonstrate geographic synchrony for the six macro-scale populations used in this study with only two years of data. In contrast to these earlier findings, our results demonstrate significant synchrony occurring in acorn production among individuals within and between populations of California black oaks up to 814 km apart, essentially throughout its range in California. Thus, spatial synchrony on a large geographic scale is not restricted to species of California oaks requiring a single year to mature acorns such as *Q. lobata* and *Q. douglasii*.

Although potential weather cues were generally not strongly correlated with acorn production at individual sites, there were fairly consistent correlations between annual acorn production and both total spring precipitation and average spring temperature for the spring two years prior to the autumn acorn crop. These relationships suggest that conditions during flowering and pollination have a significant affect on subsequent acorn production in this two-year species. Previously, Koenig and others (1999) found that mean April temperatures lagged one year were positively correlated with California black oak acorn production at one of two sites. In addition, Koenig and others (1996) were unable to find a significant relationship in California black oak annual acorn crops and 12 weather variables at one (Hastings) of the six macro-scale sites used here.

The specific component of acorn production that is influenced by spring weather is unclear (Cecich and Sullivan 1999, Koenig and others 1996, Sork and others 1993), particularly with species with acorns that require two years to mature such as that studied here. Weather conditions affect acorn production by influencing pollination, fertilization, and ovulation, and water availability may also affect flower development and acorn production in a delayed manner (Koenig and others 1996, Sork and others 1993). Pollination, fertilization, and ovulation are generally reduced during colder, wetter conditions so negative relationships should be expected to occur with California black oak acorn production. Flower survival in black oak (*Q. velutina*), a closely related species found in eastern North America, was positively correlated with the number of days of rain during the pollination period and high temperatures reduced flower survival in Missouri (Cecich and Sullivan 1999), indicating interactive effects of weather on acorn production. This compensatory relationship with *Q. velutina* may also occur with California black oak and thereby explain the relatively weak weather-acorn crop relationships found here. It is also well known that weather variables influence crop yields of nut-producing trees in California where yield declines as temperatures decrease and precipitation increases (Lobell and others 2006).

Perhaps the strongest relationships revealed here were a decrease in mean annual acorn production and an increase in variation of the annual production with increasing latitude among the seven populations, a relationship mirrored by a positive correlation between latitude and spring precipitation lagged one year. Decreasing annual variability from southern to northern latitudes is a pattern found generally among Northern Hemisphere trees (Koenig and Knops 2000). The consequences and generality of these patterns are clearly worthy of additional study with more populations and additional years of data.

California black oak is widespread across considerable latitudinal, longitudinal, and altitudinal gradients in California, so the species is subject to more environmental variability than most other California oaks. Given the great variation in acorn production among sites observed in this study, it is clear that California black oak acorn production is probably affected by many factors. This matches the earlier conclusion of Kelly and others (2001), who found that variation in acorn crops within a species varies geographically, and that the greatest variation occurred at higher altitudes and latitudes.

Koenig and others (1999) speculated that environmental factors that synchronize acorn production with California black oak are more complicated and, hence, less likely to result in synchronization of acorn crops compared to the one-year masting oak species. In addition, California black oak demonstrates a high degree of population-level variation in masting behavior where acorn crops are geographically synchronous but annually variable (Koenig and others 2003). California black oak is primarily an oak of montane environments, and hence is subjected to weather conditions that are more variable with greater extremes in temperature and precipitation potentially affecting acorn production than California oaks in lowland and foothill locations. Such factors may partially explain the considerable differences in overall productivity observed among the sites included in this study.

Mean temporal autocorrelations in acorn production were generally negative, with peak negative values occurring at two and five years. Similar strongly negative temporal autocorrelations at long time lags, including a peak at five years, were reported by Koenig and others (1994a) using *Q. kelloggii* data from Hastings

Reservation, also included in the analyses performed here. (Note that this earlier study reported non-partial temporal autocorrelations and thus the results are not directly comparable to those reported here.) Our results suggest that, to the extent there are regular cycles of acorn production in this species, cycle length is very long making them difficult to detect given the relatively short duration of our study. Data over additional years will be necessary in order to detect such long potential cycles of acorn production. These results do, however, indicate that acorn production in individual California black oaks has a significant and extremely long-lasting negative influence on acorn production for a remarkably long period of time lasting at least seven years. This suggests that acorn production in this species requires a large amount of resources and takes many years for individual trees to recoup.

In addition to weather, acorn crops of California black oak might be influenced by other proximate factors such as stand structure and tree size, variables known to affect acorn crops of oaks from the eastern United States that are closely related to California black oak, including northern red (*Q. rubra*) and eastern black oaks (Greenberg 2000, Healy and others 1999). Stand and tree variables could influence synchrony in many ways, depending on the similarities and differences in these variables, and these relationships merit further study. For example, pollination of oak flowers may be influenced by tree density such that trees in high-density stands or extremely low-density stands produce fewer acorns than trees in moderate-density stands (Knapp and others 2001). California black oak occurs in a wide range of stand conditions from woodlands to forests, and the seven populations included in this study exist under very different stand conditions. Additional work assessing the effect of such varying stand conditions, as well as individual tree characteristics on acorn production, is clearly warranted and will be necessary in order to fully understand the patterns of spatial and temporal acorn production observed in this species.

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Continue

Regeneration of Oaks and Tanoak in *Phytophthora ramorum*-Affected Forests[1]

Tedmund J. Swiecki[2] and Elizabeth A. Bernhardt[3]

Abstract

Recent mortality in coast live oak (*Quercus agrifolia*), California black oak (*Q. kelloggii*), and tanoak (*Lithocarpus densiflorus*) exceeds historical levels in forests affected by the pathogen *Phytophthora ramorum*. We assessed the balance between recent mortality and seedling populations in these species to examine the status of regeneration in stands with varying levels of mortality caused by *P. ramorum* and other agents. Regeneration data were collected from two sets of permanent 0.02 ha plots. In a set of 150 plots distributed across 12 locations where *P. ramorum* is present, seedling counts and mature tree condition were rated annually from 2000 through 2005. In a second set of 250 plots distributed across 11 locations with and without *P. ramorum* in Sonoma County, data were collected in 2001 and 2004.

Data from plots assessed annually showed that coast live oak seedling populations fluctuated more widely from year to year than did tanoak seedling populations. Across both plot sets, tanoak seedlings were consistently present in plots with tanoak trees. Consequently, nearly all plots with tanoak mortality had tanoak seedlings, which could potentially grow to replace dead trees. Coast live oak seedlings were present in about 80 percent of all plots with coast live oak trees. About 6 to 8 percent of plots with coast live oak trees had mortality but no coast live oak seedlings. Less than half of all plots with California black oak trees had California black oak seedlings. Three-quarters of the plots with California black oak mortality lacked seedlings of this species. In these forests, regeneration of California black oak appears inadequate to maintain stand density even without the additional mortality due to *P. ramorum*.

Keywords: Mortality, Phytophthora ramorum*, regeneration, sudden oak death, SOD.*

Introduction

The exotic pathogen *Phytophthora ramorum* causes bark cankers that can kill mature coast live oak (*Quercus agrifolia*), California black oak, (*Q. kelloggii*), and tanoak (*Lithocarpus densiflorus*) trees. *P. ramorum* canker, also known as sudden oak death (SOD), has recently become a major cause of tree mortality in these three species in a number of California counties (Rizzo and others 2002, Swiecki and Bernhardt 2006). By killing overstory trees of these species, *P. ramorum* canker has the potential to change the composition of infested forests over the short term. Long-term composition changes may result if overstory mortality is not replaced by trees of the same species.

Populations of seedling advance regeneration present in the understory prior to overstory tree mortality play an important role in determining whether canopy gaps created by oak or tanoak mortality will be filled by these same species. Seeding populations can vary over time due to fluctuating rates of establishment and mortality. For example, because acorn production is highly variable from year to year

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[2] Principal and Plant Pathologist, Phytosphere Research, 1027 Davis Street, Vacaville, CA 95687.

[3] Principal and Plant Pathologist, Phytosphere Research, 1027 Davis Street, Vacaville, CA 95687.

(Koenig and Knops 2005), few or no seedlings may become established in years with low acorn production.

P. ramorum is able to cause twig infections in tanoak, but not in coast live oak. Both coast live oak and tanoak seedlings developed cankers when artificially inoculated at a wound with *P. ramorum*, but tanoak developed longer cankers, and only tanoak seedlings were killed (Rizzo and others 2002). Furthermore, *P. ramorum* stem cankers do not typically occur on small-diameter coast live oak, and did not occur in trees with a bark thickness of less than 1 cm (Swiecki and Bernhardt 2005a). Therefore, tanoak appears to be susceptible to *P. ramorum* canker from the seedling stage though the mature tree stage, whereas coast live oak seedlings do not appear to be at risk of *P. ramorum* canker.

We assessed both tree mortality and seedling populations of coast live oak, California black oak, and tanoak in two separate sets of permanent study plots. The first of these studies was initiated in September 2000 as a case-control study of factors affecting disease occurrence and progress in coast live oak and tanoak (Swiecki and Bernhardt 2002, 2005a, 2006). All of these plots were established in areas where SOD was common, and have been re-evaluated annually through 2005 in order to study factors related to disease onset and progression. The second study was designed to assess SOD impacts over time to tree health in Sonoma County woodlands and forests containing these three hardwoods. These plots were established in 2001 and re-evaluated in 2004 (Swiecki and Bernhardt 2005b, these proceedings). This paper reports on seedling population data collected in these two independent studies and on the balance between advance regeneration and overstory mortality.

Methods

Plot selection

Case-control study plots

Case-control study plots were established in September 2000. A total of 150 plots were distributed across 12 study areas located primarily in Marin County (*table 1*). Plots were established in areas where *P. ramorum* had been shown to be prevalent. Study sites were selected on the basis of appropriate vegetation type (adequate representation of coast live oak or tanoak), the presence of cases (trees with symptoms of *P. ramorum* canker) and controls (asymptomatic trees) in the study area, and absence of recent disturbances that might affect tree health (e.g., root-damaging construction). Coast live oak was the subject host species at 10 of the 12 locations; tanoak was the subject species at the remaining two locations (Swiecki and Bernhardt 2002, 2005a).

***Table 1**—Study locations with numbers of plots and host species present at each.*

Location number[1]	**Location**	**Number of plots**	**Subject tree species**
1	Marin Municipal Water District (MMWD) watershed - Azalea Hill area	12	coast live oak
2	MMWD-Pumpkin Ridge south	16	coast live oak
3	MMWD-Pumpkin Ridge north	11	coast live oak
4	MMWD-Phoenix Lake area	11	coast live oak
5	China Camp State Park - Miwok Meadows area	16	coast live oak
6	China Camp State Park - SE Buckeye Point area	12	coast live oak
7	Woodacre (Private land)	12	coast live oak
8	Lucas Valley (Private land)	12	coast live oak
9	Muir Woods NM / Mt. Tamalpias SP	10	tanoak
10	Wall Road (Private land)	13	coast live oak
11	Novato (Private land)	13	coast live oak
12	Jack London State Park	12	tanoak
2-1	Jack London State Park[2]	24	Cal. black oak, tanoak, coast live oak
2-2	Sugarloaf Ridge State Park	25	coast live oak
2-3	Lake Sonoma (Army Corps of Engineers)	24	coast live oak, Cal. black oak
2-4	Weston (private land)	26	coast live oak, Cal. black oak
2-5	Austin Creek State Recreation Area	25	tanoak, Cal. black oak
2-6	Modini (private land)	25	Cal. black oak, coast live oak
2-7	Annadel State Park	24	Cal. black oak
2-8	Salt Point State Park	18	tanoak
2-9	Helen Putnam Regional Park	24	coast live oak, Cal. black oak
2-10	Foothill Regional Park	15	Cal. black oak, coast live oak
2-11	Sonoma Coast State Beach	21	tanoak

[1] Study locations 1 through 12 are from the case-control study, and except for locations 10 (Napa County) and 12 (Sonoma County) are located in Marin County. Locations 2-1 through 2-12 are from the Sonoma County study.

[2] Study locations 12 and 2-1 were in different areas of Jack London State Park, separated by about 1 km and differing in elevation by about 170 m.

At each study location, we established 10 to 16 circular 8 m radius (0.02 ha=0.05 acre) fixed-area plots, each of which was centered at a subject tree. Interplot spacing varied with vegetation and terrain and the distribution of plots across the landscape varied by location. To avoid overlap between plots, no two adjacent plot centers were located closer than 16 m apart; centers of most adjacent plots were separated by 20 to 30 m.

Each tree in each plot was identified by distance and azimuth from the plot center and by DBH. We evaluated the disease status and condition of all coast live oak, California black oak, and tanoak trees (DBH≥3 cm) in the plots every September from 2000 through 2005 (Swiecki and Bernhardt 2002, 2005a). In the initial (2000) evaluation, dead oaks and tanoaks were counted only if it appeared that they had died within the previous 10 years.

At each assessment, the likely cause of recent tree mortality was determined. Confirmation of *P. ramorum* from selected trees was made by culturing tissue pieces on PARP agar media (Swiecki and Bernhardt 2005a).

Seedlings (DBH<3 cm) of coast live oak, California black oak, and tanoak were counted in each plot in September each year using hand tally counters. If live seedlings of any species were too numerous to tally, numbers of seedlings were estimated. For other forest canopy species, seedlings in plots (plants up to 3 cm DBH) were not counted but were noted as present or absent only in 2000.

Sonoma County Study Plots

In 2001, we established 250 plots at 11 locations throughout Sonoma County to monitor forest health and the spread of *P. ramorum* (Swiecki and Bernhardt 2005b, these proceedings). Locations were chosen in areas where tanoak, coast live oak, and/or California black oak were common (*table 1*).

Plots at each location were established at vertices of a grid superimposed over a map of the location and are unbiased with respect to tree condition or the presence or absence of *P. ramorum* canker. The only requirements for establishing a plot at a grid intersection was that coast live oak, California black oak, and/or tanoak were present and the slope was navigable (generally no greater than about 70 percent). Plot selection and placement details are given in Swiecki and Bernhardt (these proceedings).

Plots were the same type as those in the case-control study described above (0.02 ha circular plots) except that plots were centered at random points rather than at trees. The nominal spacing between grid points was 50 m as plotted on a topographic map, with the exception of the first location (Jack London SP) where the grid spacing was 60 m. Because only plots containing coast live oak, California black oak, and/or tanoak were sampled, the pattern of actual plot positions often differs from the idealized sampling grid. In addition, the overall area represented by the sampled plots in each grid varied between locations, from about 4.7 to 14 ha, depending on the distribution of the host trees at each location.

We collected the same data on tree (DBH≥3 cm) disease status and condition and the presence of seedlings in plots as described for the case-control plots above, but plots were evaluated only in the summers of 2001 and 2004. As described above, we isolated from symptomatic coast live oak, California black oak, tanoak, California bay and some other host species to confirm the presence of *P. ramorum* or other *Phytophthora* species within plots.

Data Management and Analysis

Data summaries and analyses were prepared using JMP statistical software version 5.1.2 (SAS Inc., Cary NC). The square root transformation was applied to seedling count data prior to analysis of variance. Tukey-Kramer HSD was used to test for differences between multiple means. Repeated-measures analysis of variance was used to test for factors related to changes in annual seedling counts. Unless otherwise indicated, effects or differences are referred to as significant if $p \leq 0.05$.

Results

Seedling Populations

Coast Live Oak

Among the 10 coast live oak locations in the case-control study in forests affected by *P. ramorum* and monitored every September between 2000 and 2005, seedling numbers fluctuated widely, both among plots at the same location, and within the same plots from year to year (*fig. 1*). In half of the plots, the maximum number of coast live oak seedlings observed in any year was 10 or less, which corresponds to a seedling density of 500 seedlings/ha or less (1 seedling per plot equals 50 seedlings per ha).

The year 2001 marked a peak in seedling numbers (*fig. 1, table 2*). Seven of the 10 locations had peak seedling populations in 2001, the only year in which average seedling counts per plot differed from other years (*table 2*). In locations that showed strong increases in seedling counts in 2001 compared to 2000, the mean number of seedlings per plot has decreased in subsequent years. It appears that this decrease is due to mortality of many of the seedlings established in 2001.

We used a repeated measures analysis of variance of plot seedling counts to determine whether various factors were associated with changes in seedling populations over time. These analyses indicate that seedling counts varied significantly over time and between locations (F test $p<0.0001$ for both factors) and are somewhat negatively correlated with the number of live coast live oak trees in the plot (F test $p=0.0265$). The interaction between location and time was also highly significant (Pillai's Trace, Wilk's Lambda $p<0.0001$). Factors that were not significantly related to seedling population levels included whether coast live oaks with *P. ramorum* canker symptoms were present in the plot, the number of dead coast live oak trees in the plot, overall plot canopy cover, and shrub cover in the plot.

The Sonoma County plots were evaluated in 2001 and 2004. As in the case-control plots, seedling populations were significantly lower in 2004 than they were in 2001 (*tables 2, 3*). We used repeated measures analysis of variance models to test for differences in coast live oak seedling counts for 2001 and 2004 using data from both the Sonoma and case-control plot sets. As was seen in the analysis of the 2000 through 2005 data from the case-control plots, the effects of time (2001 vs. 2004), location, and the time by location interaction were significant in models using all coast live oak plots from both plot sets (F test $p<0.0001$ for all). Plot set (Sonoma vs. case-control) was not significant, indicating that overall coast live oak seedlings densities did not differ significantly between the two sets of plots overall, despite the significant differences between various locations. None of the other factors tested, including the number of live or dead coast live oak trees or the presence of *P. ramorum* canker symptoms in the plot, significantly affected seedling counts.

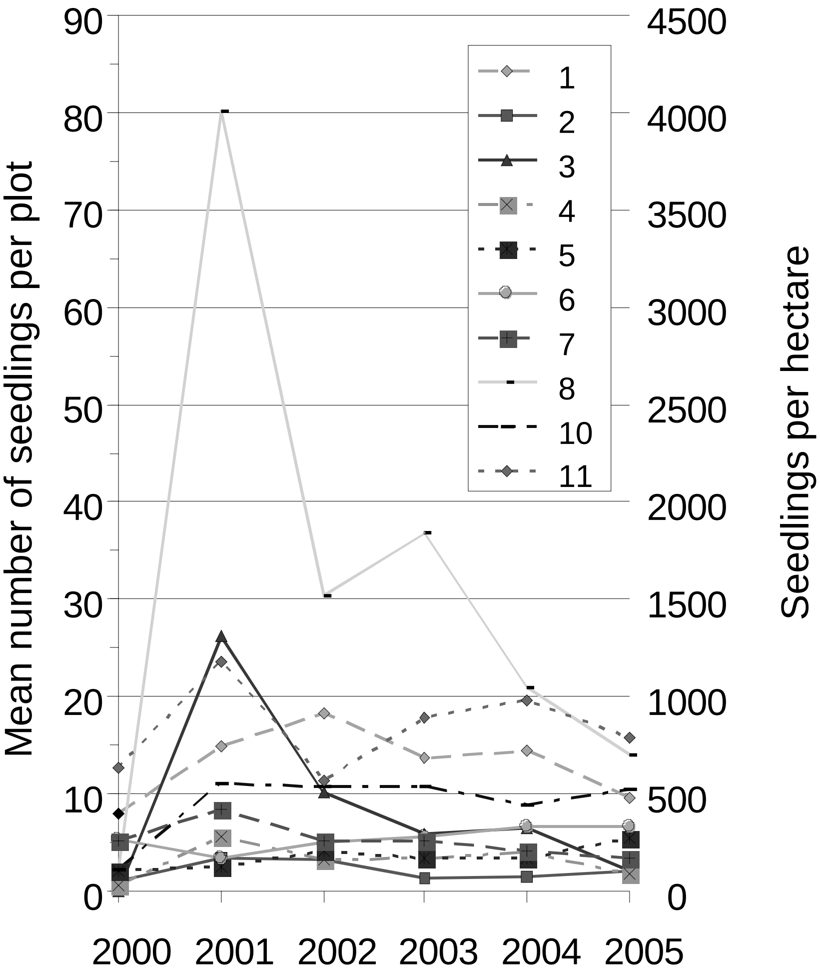

Figure 1—Mean numbers of coast live oak seedlings per plot at each of 10 case-control study locations with coast live oak overstory. Seedling counts were made in September of each year. Location numbers in the legend are the same as in Table 1.

Table 2*—Mean (and standard deviation) of coast live oak seedling or tanoak seedling counts per plot by year in case-control study plots. Coast live oak means are calculated from 125 plots with coast live oak seedlings in at least one year. Tanoak means are calculated from 39 plots that either have tanoak overstory (25 plots) or lacked tanoak overstory but had tanoak seedlings present in at least one year (14 plots).*

Year	2000	2001	2002	2003	2004	2005
Coast live oak	4.0 (5.9)	17.3[1] (32.3)	10 (15.9)	10.2 (20.7)	8.8 (11.4)	7.2 (9.2)
Tanoak	11.8 (13.4)	11.5 (9.5)	13.8 (12.9)	13.1 (13.3)	12.4 (10.3)	13.8 (12.3)

[1] significantly different from means from all other years for this species according to Tukey-Kramer HSD.

Table 3—Mean counts of seedlings (<3 cm DBH) per plot by species in Sonoma County study plots that had seedlings of the species present in 2001 and/or 2004.

Species	**Number of plots**	**2001 mean seedlings/plot (SD)**	**2004 mean seedlings/plot (SD)**
Tanoak	85	22.0 (19.0)	23.1 (20.7)
Coast live oak[1]	119	19.3 (26.9)	11.5[2] (18.1)
California black oak	78	3.7 (8.0)	2.7 (4.1)

[1] Coast live oak means exclude 15 plots with estimated regeneration counts greater than 100 per plot in 2004. Estimated counts in these plots were the same in both 2001 and 2004.

[2] Significantly different from 2001 mean at p<0.0001 (two-tailed paired t-test).

The number of dead coast live oak seedlings tallied in the case-control plots each year was almost always much smaller than the drop observed in live seedling numbers from one year to the next. Many small dead seedlings apparently did not persist long enough to be observed in annual evaluations. Presumably, at least some of these may have been destroyed by herbivores. Hence, counts of dead coast live oak seedlings within plots did not provide an accurate picture of seedling mortality from year to year.

California Black Oak

Both overstory trees and seedlings of California black oak were uncommon in the case-control study plots. Counts of black oak seedlings were initiated in 2001, at which time only five plots at four locations had California black oak seedlings present (one to three seedlings per plot). By 2005, only two plots at two locations had California black oak seedlings (one seedling in each plot). These seedlings were not in plots with overstory California black oaks.

In the Sonoma County study, nine locations had California black oak trees. Seedling populations per plot were very low and the average number of seedlings per plot did not change significantly from 2001 to 2004 (*table 3*). Two plots at Weston had an estimated 50 seedlings in 2001, which were reduced to counts of 15 and 2 by 2004. The highest number of California black oak seedlings per plot in 2004 was 24, and only 10 percent of the plots with California black oak regeneration had more than 15 seedlings.

Tanoak

Tanoak twigs are susceptible to *P. ramorum* and understory tanoak seedlings commonly showed tip dieback and/or mortality of individual stems. However, over the period of the case-control study, this damage has not resulted in a reduction in tanoak seedling populations at the three locations that had tanoak seedlings present. According to a repeated measures analysis of variance on the case-control plot data, seedling counts per plot have not changed significantly between 2000 and 2005. The effect of location was significant (F test p=0.0025), but the time by location interaction was not significant.

Tanoak seedling counts in the Sonoma County plots showed a similar trend. The average number of seedlings per plot did not change from 2001 to 2004 (*table 3*). Repeated measures analysis of variance models using all tanoak plots from both the case-control and Sonoma data sets for 2001 and 2004 also showed no significant effect of time on tanoak seedling counts. Tanoak seedling counts did differ significantly by location (F test p<0.0001), and counts were higher overall in the

Sonoma plots than in the case-control plots (F test p=0.0015). Other factors tested, including the numbers of live or dead tanoak trees or the presence of *P. ramorum* canker symptoms in the plot, were not significantly related to tanoak seedling counts in these models.

Among all plots with tanoak seedlings in both plot sets, the maximum number of seedlings per plot in 2004 was estimated at 100 (5,000 seedlings/ha) and half of the plots had 20 or more seedlings (1,000 seedlings/ha). For the Sonoma plots, tanoaks had the highest and California black oak the lowest seedling counts per plot in 2004, and differences in the average number of seedlings per plot for the three species were significant (Tukey's HSD, p=0.05). However, this result was only obtained if the 15 plots with very high coast live oak seedling counts (150 to 1,000 per plot) were omitted from the analysis (*table 3*). Including these 15 plots gives coast live oak the highest numerical average overall (48 seedlings per plot), but due to the high variance, coast live oak and tanoak seedling counts did not differ significantly from each other.

Distribution of Seedlings Among Plots

Almost all of the case-control study plots with coast live oak overstory had coast live oak seedlings at some point between 2000 and 2005. Only five of these 128 plots had no coast live oak seedlings in any of the six years of the study. However, 46 percent of these plots had no coast live oak seedlings in at least one year. Coast live oak seedlings were also found in plots that lacked coast live oak trees. In 2004, 36 of 156 plots from both plot sets without coast live oak trees had seedlings of this species.

The percent of case-control plots with coast live oak seedlings increased greatly from 2000 to 2001 (*fig. 2*), paralleling the increase in average seedling numbers per plot seen in 2001 (*fig. 1, table 2*). After 2001, the percent of plots with seedlings decreased slightly, but more plots had seedlings in 2005 than in 2000 (*fig. 2*). In the Sonoma plots, the percentage of plots with coast live oak seedlings decreased slightly from 2001 to 2004, and was similar to the percentages from the case-control study for the corresponding years (*fig. 3*).

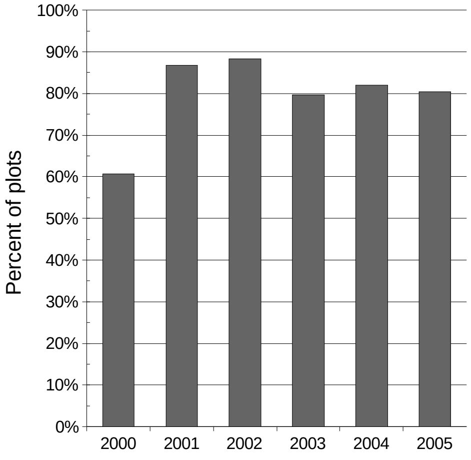

Figure 2—Percent of plots with coast live oak seedlings in September of the year shown.

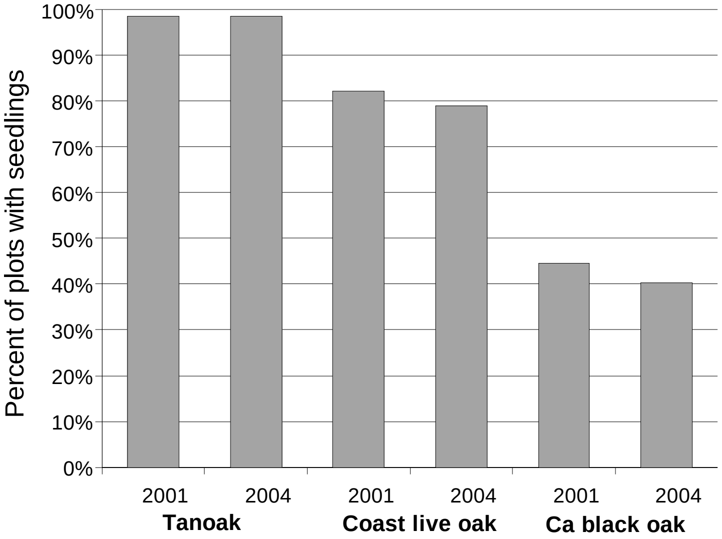

Figure 3—Percent of Sonoma County study plots with regeneration of the same species in 2001 and 2004. Tanoak (73 plots), Coast live oak (114 plots), California black oak (119 plots).

California black oak seedlings were present in less than half of the Sonoma County plots with canopy trees of this species, and the percentage of plots with California black oak seedlings decreased between 2001 and 2004 (*fig. 3*). Hence, California black oak showed both low seedling densities within plots and relatively low constancy within plots with overstory trees. Nonetheless, California black oak seedlings were found in 15 of 270 plots from both plot sets that lacked California black oak canopy.

In contrast, tanoak seedlings were present in almost all plots with tanoak trees. Tanoak seedlings were present in 23 or more of the 25 plots of the case-control plots with tanoak trees between 2000 and 2005. Nearly all of the Sonoma plots with tanoak trees also had tanoak seedlings present in both 2001 and 2004 (*fig. 3*). In 2004, tanoak seedlings were also found in 24 of 302 plots from both sets that had no tanoak canopy.

Seedling Form and Growth

The overwhelming majority of coast live oak seedlings in the plots were very small, typically less than 10 cm tall, and commonly had only one or two stems from the ground. Rarely, very high numbers of these small seedlings were found in plots. Helen Putnam RP was unique in having many plots with very high numbers of seedlings per plot (estimated up to 1,000 per plot). A few larger seedlings, generally up to about 30-cm tall, were found in a few plots at various locations. These larger seedlings were generally multistemmed and shrubby in appearance. In plots that have experienced significant canopy loss due to tree mortality and/or failure over the course of the study, larger shrubby seedlings have become more common, and some of these were up to about 50-cm tall in 2005. Such seedlings are often, but not exclusively, found near or among failed branches and other woody debris that provide some protection from deer browsing. However, none of coast live oak seedlings in either plot set have grown large enough to advance to the tree size class (at least 3 cm DBH).

California black oak seedlings within plots were also typically small (<30 cm) and mostly single-stemmed. We did not observe larger shrubby forms, as seen in coast live oak and tanoak, among California black oak advance regeneration. None of the California black oak seedlings in either plot set has been recruited to the tree stage over the study period.

Tanoak seedlings were normally larger than coast live or California black oak seedlings. Most tanoak seedlings were 30- to 60-cm tall, but some were more than 150-cm tall; smaller seedlings (<30 cm) were also present in some areas. Tanoak advance regeneration most commonly occurred as shrubby seedling-sprouts with multiple stems. Although individual shoots of these seedling-sprouts commonly died back to ground level, we observed relatively few of these larger seedlings that died completely over the course of the two studies. Three tanoak seedlings in the case-control plots, and 14 in the Sonoma plots grew to attain a DBH of 3 cm or more over the respective study periods and are now classified as trees for purposes of data collection.

Balance Between Tree Mortality and Seedling Presence

Coast Live Oak Plots

Plot-level data on tree mortality was compared with seedling counts to provide a measure of the adequacy of advance regeneration. If overstory mortality was present within a plot but understory seedlings of the same species were lacking, we considered that the level of advance regeneration was probably inadequate.

In the case-control plots, the percent of coast live oak plots with at least one dead coast live oak tree nearly doubled between 2000 to 2005 (*fig. 4*). Because the case-control study plots were all in areas affected by *P. ramorum*, 69 percent of the mortality occurring over this interval was due to *P. ramorum*. Over the same interval, the percentage of coast live oak overstory plots with coast live oak seedlings also increased (*fig. 3*). Due to the increase in the number of plots with seedlings, the percentage of plots that had coast live oak overstory mortality but no coast live oak seedlings decreased slightly over this time interval (*fig. 4*). Hence, by this simple metric, it appears that the potential for coast live oak mortality to be replaced though regeneration in these plots has not changed substantially between 2000 and 2005. Although coast live oak seedlings in some plots with recent mortality-related canopy gaps have grown substantially, none of these seedlings have grown large enough to escape browsing of the leader by deer.

In the Sonoma plots, the percent of coast live oak plots with at least one dead coast live oak tree increased between 2001 and 2004 (*fig. 4*). Only four of the nine Sonoma study locations with coast live oak trees also had *P. ramorum* canker present; 39 percent of the coast live oaks that died during this interval were killed by *P. ramorum*. Over the same interval, the percentage of plots with coast live oak seedlings decreased slightly (*fig. 3*). This resulted in a slight increase in the percent of plots with coast live oak overstory mortality but no coast live oak seedlings (*fig. 4*).

California Black Oak Plots

Sixteen California black oak trees were present in 11 of the case-control plots at six locations. Three of these trees died between 2000 and 2005; two of the deaths were due to *P. ramorum*. None of the plots with California black oak trees had California black oak seedlings, so it appears unlikely that California black oak regeneration would replace any of these killed trees.

Among the Sonoma plots, the percentage of plots with California black oak mortality doubled from 2001 to 2004 (*fig. 4*). Five of the nine locations with California black oaks also had *P. ramorum* canker, and 25 percent of the California black oaks that died between 2001 and 2004 were killed by *P. ramorum.* The number of plots with California black oak mortality that lacked seedlings increased three-fold between 2001 and 2004 *(fig. 4*).

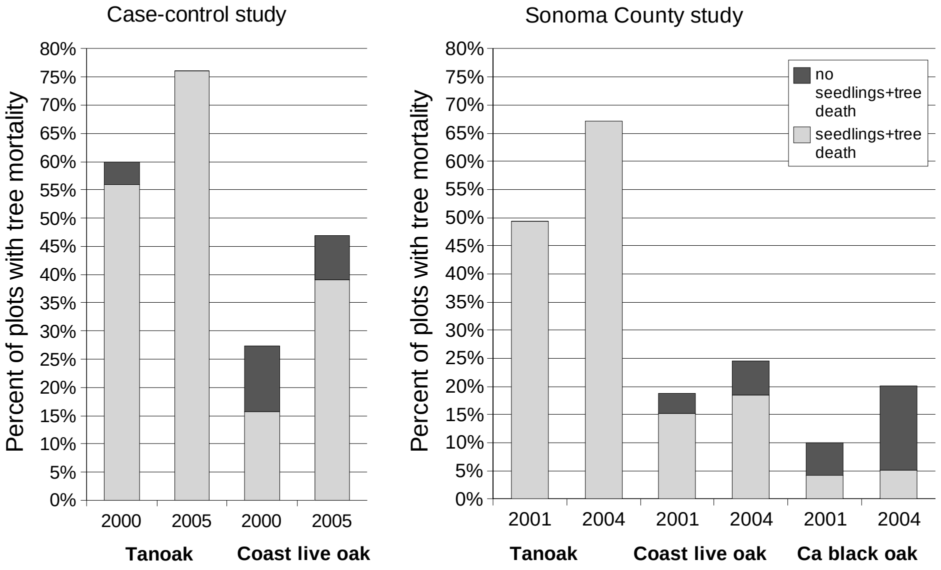

Figure 4—Percent of plots with and without tree mortality and regeneration of the same species in 2001 and 2004. The case-control study includes 28 plots with tanoak and 128 plots with coast live oak trees. The Sonoma County study includes 73 plots with tanoak, 114 plots with coast live oak, and 119 plots with California black oak trees.

Tanoak Plots

Among the case-control study plots with tanoak trees, mortality increased substantially between 2000 and 2005 (*fig. 4*). *P. ramorum* canker*,* which was present at all locations with tanoaks, killed 76 percent of the tanoaks that died between 2000 and 2005. However, by 2005, all case-control plots with tanoak mortality also had tanoak seedlings (*fig. 4*).

Two of the four Sonoma study locations with tanoak trees were confirmed to have *P. ramorum* canker, but tanoaks at the other two locations are affected by an unidentified canker disease (Swiecki and Bernhardt, these proceedings). The percent of Sonoma plots with mortality of tanoaks increased substantially between 2001 and 2004 (*fig. 5*); 36 percent of the tanoaks that died during the interval had *P. ramorum* canker. All of the plots with dead tanoak trees also had tanoak seedlings in both 2001 and 2004.

Seedlings of Other Tree Species

In the case-control plots, we recorded whether seedlings of other forest canopy species were present in plots in 2000. California bay (*Umbellularia californica*) regeneration was observed in 67 percent of the study plots. The other most commonly observed seedlings were Douglas-fir (*Pseudotsuga menziesii*), in 43 percent of the plots, and madrone (*Arbutus menziesii),* in 16 percent of plots. In the Sonoma plots, seedlings of other forest canopy species in plots were noted as present or absent in both 2001 and 2004, although no significant changes were observed over this interval. California bay seedlings were found in 64 percent of the Sonoma plots. Other canopy species commonly represented as seedlings in the Sonoma plots included Douglas fir (49 percent of plots), madrone (28 percent of plots), coast redwood (*Sequoia sempervirens*) (12 percent of plots), and bigleaf maple (*Acer macrophyllum*) (9 percent of plots). All of these other species are susceptible to foliar or twig blighting caused by *P. ramorum*.

Discussion

Regeneration involves replacement of existing trees that die. For oaks and tanoaks, most of this replacement occurs via persistent seedlings (advance regeneration) that have become established in the understory. These seedlings are typically not released until a gap in the canopy is created or suppressive effects of overstory trees are otherwise reduced.

Tanoak seedlings in both studies were present in a range of size classes, but much of this advanced regeneration consisted of “seedling-sprouts” (Burns and Honkala 1990). These are small, shrubby plants that form from seedlings whose shoots have periodically died back to the ground and been replaced by new shoots arising from the root crown or basal burl. Due to its understory tolerance and growth form, tanoak advance regeneration was consistently larger than coast live oak and California black oak advance regeneration observed in the plots. Overall, it appears that these smaller oak seedlings did not persist in the understory as long as did the larger tanoak seedlings.

Tanoak seedlings also showed better growth in the understory than the oaks. At least 17 of the taller understory tanoak seedlings attained a DBH of 3 cm or more during the course of the two studies. In contrast, no oak seedlings were recruited to the tree stage, and the best growth was seen among coast live oak seedlings that were in recent canopy gaps.

The density of coast live oak seedlings within plots varied much more widely over time than did tanoak or California black oak seedling densities. From the case-control study data, it appears that large numbers of coast live oak seedlings became established in some years, such as in early 2001 (*fig. 1*). This is probably related in part to a good acorn supply in the preceding fall. The fall 2000 acorn crop for coast live oak had the highest counts recorded for the period from 1993 through 2005 in an annual mast survey of California oaks (W. Koenig and J. Knops, unpublished). Many of the new seedlings established after this heavy mast year apparently did not survive for more than one to two years (*fig. 1*). Because mast production for a given oak species is typically similar over a relatively wide geographic area (Koenig and Knops 2005) it is likely that the decline in seedling numbers in 2004 compared to 2001 seen in the Sonoma plots represents the same phenomenon seen in the case-control plots.

The comparison between mortality and seedling presence indicated that coast live oak mortality has the potential to be replaced by regeneration in most of the study plots (*fig. 4, 5*). However, considering the small size and limited persistence of coast live oak advance regeneration, there is no guarantee that sufficient numbers of seedlings present in these plots will survive long enough to be recruited. Coast live oak seedling counts in plots were generally low, averaging less than 10 seedlings per plot in case-control plots and just slightly higher in Sonoma County locations (*tables 2, 3*).

Furthermore, recruitment of coast live oak seedlings appeared to be strongly dependent on canopy gaps. Due to the high stocking levels found in many of the stands, relatively small canopy gaps may be refilled relatively quickly through growth of remaining overstory or understory, possibly inhibiting coast live oak seedling recruitment. Even if canopy gaps are large enough and relatively long-lived, virtually all of the stands we studied also had regeneration of various tree canopy species present. Faster growing species, such as Douglas fir, may overtop and suppress coast live oak regeneration in these gaps, especially at more mesic sites. Hence, it is likely that long-term reductions in coast live oak stand density may occur in more than the 6 to 8 percent of coast live oak plots that have recent coast live oak mortality and lack coast live oak regeneration.

The regeneration data gathered to date indicates that among the SOD canker hosts studied in the Sonoma plots, California black oak populations are currently at greatest risk of decline as the result of non-replaced overstory mortality. The case-control study does not include enough California black oak to draw strong conclusions. However, it is unlikely that California black oaks killed by *P. ramorum* in the case-control plots will be replaced by regeneration of this species. Due to sparse seedling production by California black oak, long-term losses in the density of this species are likely to occur in stands with even low levels of mortality due to *P. ramorum*. Indeed, current levels of advance regeneration in California black oak appear to be inadequate to offset tree mortality due to agents other than *P. ramorum*.

In contrast, the potential for tanoak regeneration currently appears to be quite robust, at least at the locations we studied. Even though tanoak seedlings are susceptible to *P. ramorum* canker, seedling population data collected to date do not indicate that *P. ramorum* has significantly impacted seedling tanoak populations within areas where this pathogen has become established. However, continued long-term monitoring will be needed to determine whether tanoak seedlings will be able to recruit to the tree size class in areas with high levels of *P. ramorum* inoculum. Although we have seen some tanoak seedlings grow to attain diameters of 3 cm or more over the study period, tanoak stems in this diameter class are susceptible to *P. ramorum* (Rizzo and others 2002) and may be killed before they attain reproductive age. Ultimately, the ability of tanoak to regenerate in areas affected by *P. ramorum* may depend on the prevalence of resistant genotypes within the pool of advance regeneration.

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Timing of Flowering and Seed Production in Three California Oaks[1]

Walter D. Koenig,[2] Johannes M.H. Knops,[3] and William J. Carmen[4]

Abstract

We examined the importance of pollen limitation to variation in acorn production of three species of California oaks (*Quercus lobata*, *Q. douglasii,* and *Q. agrifolia*) by testing for relationships between phenology and acorn production. Within years, trees flowering closer to the mean flowering date of the population produced significantly more acorns in two of the species. Assuming that more pollen is available when more conspecifics are blooming, this result is consistent with pollen limitation affecting individual variation in acorn productivity. Across years, relatively warm, dry conditions during the peak of flowering correlated with larger acorn crops the following fall in all three species. Assuming that such conditions favor either increased pollen movement or increased fertilization, this is consistent with the hypothesis that pollen limitation plays a significant role in the highly variable seed crops characteristic of masting in these species. Overall, the proportion of total variance in the acorn production of individual trees explained by these two indices of pollen availability ranged from 28 to 38 percent. These results support the hypothesis that pollen limitation plays an important role in causing variance in seed production in these wind-pollinated oaks.

Keywords: Acorn production, masting, phenology, pollen limitation.

Introduction

Wind-pollinated trees cover huge areas throughout temperate and boreal regions and have vast economic and environmental importance. Many wind-pollinated trees are also notable for producing seed crops that combine high variability among individuals within years, high variability among years, and synchronized production over large geographic areas, the latter two features characterizing masting or mast-seeding (Norton and Kelly 1988; Koenig and Knops 1988; Kelly and Sork 2002).

Of central interest is the role that pollen limitation plays in these phenomena. Theoretical models have demonstrated that pollen limitation, in conjunction with environmental fluctuations, can potentially play a pivotal role in producing highly variable and synchronized patterns of seed production in wind-pollinated species (Satake and Iwasa 2000, 2002). Empirically, prior work has found that weather conditions during flowering can have a significant influence on subsequent seed production in various wind-pollinated trees (Sharp and Sprague 1967; Sork and others 1993; Koenig and others 1996; Koenig and Knops 2002), a finding that is likely to be due to effects of weather on pollen flow, although this has yet to be

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[2] Research Zoologist, Hastings Reservation and Museum of Vertebrate Zoology, University of California Berkeley, 38601 E. Carmel Valley Road, Carmel Valley, CA 93924. e-mail: koenigwd@berkeley.edu

[3] Associate Professor, School of Biological Sciences, 348 Manter Hall, University of Nebraska, Lincoln, NE 68588.

[4] 145 Eldridge Ave., Mill Valley, CA 94941.

definitively demonstrated (Koenig and Ashley 2003). To the extent that similar weather conditions affect all trees in a population, it is further possible that pollen limitation plays an important role in masting behavior.

Pollen limitation may also play an important role in causing variation in seed production among individuals within a population, as suggested by a correlation between spacing and seed production in European beech (*Fagus sylvatica*) and yew (*Taxus canadensis*) (Nilsson and Wästljung 1987; Allison 1990b), increased seed production with the addition of supplemental pollen in low-density stands of yew (Allison 1990a), and, more recently, a correlation between the number of pollen-producing neighbors and seed production in blue oaks (*Quercus douglasii*) (Knapp and others 2001). These studies all suggest that some of the variation in seed productivity among individuals may be due to differences in pollen availability.

Here we approach this issue by examining the relationship between flowering phenology and subsequent acorn production in three species of California oaks with the goal of estimating the potential importance of pollen limitation as a cause of variation in acorn production. We also analyze the relationship between mean annual acorn production and environmental conditions during the spring flowering period as a measure of the potential importance of annual differences in pollen transfer in determining year-to-year variability in acorn production.

Methods

Study Site and Species

We conducted the study at Hastings Reservation in central coastal California, where we have long-term data on acorn production by oaks since 1980. Weather records were taken from reserve headquarters, within 1.5 km and 100 m elevation of trees included in the analyses. Species included in the study were *Q. lobata* (valley oak) and *Q. douglasii* (blue oak), both members of the “white oak” subgenus Quercus, and *Q. agrifolia* (coast live oak), a member of the “black oak” subgenus Erythrobalanus. All three of these are “1-year species” requiring a single season to mature acorns. Thus, acorns counted were in all cases fertilized the prior spring.

Acorn Survey

We estimated relative acorn abundance for 86 *Q. lobata*, 56 *Q. douglasii*, and 63 *Q. agrifolia* every fall between 1980 and 2002 (23 years) using visual surveys conducted in early September. At each tree, two observers scanned different parts of the canopy and counted as many acorns as they could in 15 s. Counts were added and log-transformed to reduce the correlation between the mean and variance (Sokal and Rohlf 1981). Details of these methods are given elsewhere (Koenig and others 1994a, 1994b; Garrison and others 2008).

Phenological Survey

We performed phenological surveys on a subset of 67 trees (25 *Q. lobata*, 23 *Q. douglasii*, and 19 *Q. agrifolia*) during the six years from 1991 and 1996. We focused on male flowers (catkins), which we visually surveyed weekly starting in early March until the end of flowering in May. We recorded the date on which each tree was first in bloom as indicated by the presence of pendant male catkins and expanded flower buds, the date on which each tree ended male flowering as indicated by the absence of catkins shedding pollen, and the date when flowering peaked. Because female flowers are cryptic, we did not survey them directly. In general, however, female flowering in oaks is correlated with the period catkins are present, with the former appearing 5 to 10 days after catkins (Sharp and Sprague 1967).

In order to look for a potential effect of pollen limitation on annual acorn production, we extended prior analyses correlating overall acorn production with environmental conditions during the main flowering period the prior spring, specifically the month of April, during which 72 percent of flowering takes place in this population (Koenig and others 1996). As a comparison of the relative importance of pollen limitation vs. endogenous energy reserves in determining the mean annual acorn crop, we performed multiple regressions of environmental conditions in April and the prior year's acorn crop on the current year's acorn production.

Statistical Methods

We tested for consistency among the phenology of individuals across years using Kendall's coefficient of concordance. In order to test for pollen limitation within years, we looked for a relationship between phenology and acorn productivity of individual trees. Specifically, we assumed that there would be less pollen early and late in the season and thus tested whether trees flowering in the middle of the season produced more acorns than trees flowering early/late. We did this by using the number of standard deviations before or after the mean date individual trees flowered (the absolute value of standard deviation, |SD|) as a measure of how far from the presumed peak of pollen availability each tree flowered, regardless of whether it flowered earlier or later than the peak itself. We then performed ANOVAs with (log-transformed) acorns counted as the dependent variable, year as a main factor, and |SD| as a covariate in order to test whether acorn production of individual trees was influenced by phenology.

To compare the relative importance of conditions during pollination vs. endogenous energy reserves related to the prior year's crop, we compared the significance and change in R^2 values for regressions of the mean (log-transformed) acorn crop on mean conditions during April and the prior year's mean acorn crop separately and together using all 23 years of data and all individuals surveyed on the study site. We used analogous regressions of relative date of initial flowering and mean maximum April temperature on the subsequent acorn crops of individual trees combining the six years of phenological data to estimate the overall proportion of variance in acorn production potentially explainable by pollen limitation.

Results

Variation in Flowering

For all species, the three phenology variables (date of first flowering, date of maximum flowering, and last date of flowering) were highly correlated (nine pairwise correlations, all $r_s \geq 0.70$, all $P < 0.001$). Thus, except where noted, we present only results using the date of first flowering.

Among years, the mean date of first flowering ranged from March 4 to 29 in *Q. lobata* (26 days), March 3 to April 3 in *Q. douglasii* (31 days), and March 5 to April

16 in *Q. agrifolia* (41 days). Within years, estimated date of first flowering among individuals differed by 21 to 35 days in *Q. lobata*, 21 to 30 days in *Q. douglasii*, and 15 to 43 days in *Q. agrifolia*. Across years, however, all three measures of flowering phenology were highly significantly concordant for all three species (nine tests, Kendall's $W \geq 0.44$, all $P < 0.001$). Thus, trees tended to flower in the same relative temporal order from one year to the next, despite differences in flowering among years.

Effect of Spring Conditions on Acorn Production

Across the entire 23 years of the study, the mean acorn crop was significantly correlated with conditions during April, the peak of the flowering period, for both *Q. lobata* and *Q. douglasii*, with larger acorn crops occurring in warmer and drier springs (*table 1*). Spring conditions were not significantly correlated with acorn production in *Q. agrifolia*. The prior year's acorn crop was inversely correlated with the current crop in all three species, significantly so for *Q. lobata* and *Q. douglasii*.

Table 1—*Spearman rank correlations of the mean acorn crop vs. environmental conditions during the prior April and the mean acorn crop the prior year*[1]

Variable	*Q. lobata* (N = 86)	*Q. douglasii* (N = 56)	*Q. agrifolia* (N = 63)
Mean max. temp.	0.80***	0.60**	0.31
Mean min. temp.	0.60**	0.43*	0.07
Mean ave. temp.	0.78***	0.59**	0.26
Mean rainfall	-0.42*	-0.34	-0.01
Prior year's crop	-0.47*	-0.50*	-0.36

[1] N = 23 years (22 for the prior year's acorn crop). * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Using the environmental factor most strongly correlated with acorn production (mean maximum April temperature), environmental conditions were far more important as an explanatory variable of the current acorn crop than the prior year's acorn crop in both *Q. lobata* and *Q. douglasii* (*table 2*; neither variable was significant for *Q. agrifolia*, which is not included in the table). Adding the prior year's acorn crop to a regression of the current acorn crop on mean maximum April temperature increased R^2 values by only 3.5 percent (*Q. lobata*) and 6.4 percent (*Q. douglasii*), while adding the mean maximum April temperature to a regression of the current acorn crop on the prior year's acorn crop increased R^2 values by 43.2 percent (*Q. lobata*) and 33.3 percent (*Q. douglasii*)(*table 2*).

Table 2—*Results of multiple regressions examining the effects of mean maximum April temperature and the (log-transformed) mean prior year's acorn crop on subsequent mean acorn production (N = 23 years)*

Species (*N* individuals)	**Model**	**Adjusted R^2**	***t*-value**	***P*-value**
Q. lobata	Prior year's acorn crop only	0.188	2.4	0.025
(86)	Mean max. April temp. only	0.585	5.5	<0.001
	Both variables	0.620		
	Prior year's acorn crop		1.7	0.106
	Mean max. April temp.		4.9	<0.001
Q. douglasii	Prior year's acorn crop only	0.152	2.2	0.041
(56)	Mean max. April temp. only	0.421	4.0	0.001
	Both variables	0.485		
	Prior year's acorn crop		1.8	0.083
	Mean max. April temp.		3.7	0.001

Individual Variation, Phenology, and Acorn Production

For *Q. lobata* and *Q. agrifolia*, but not *Q. douglasii*, timing of flowering relative to the population at large was significantly related to subsequent acorn production by individual trees after controlling for differences among years (*table 3*). In both species where it was significant, acorn production increased as trees flowered closer to the overall mean flowering date. However, the proportion of variance explained by the timing of flowering was small in comparison to differences among years. Compared to analyses in which year alone was included in the model, R^2 values increased by only 1.1 percent in *Q. lobata* and 1.3 percent in *Q. agrifolia* when timing of flowering was included in the analysis. Timing of flowering did not significantly correlate with subsequent acorn production without controlling for year.

Table 3—*Results of ANOVAs examining the effects of year and date of initial flowering (relative to the overall distribution) on subsequent acorn production of individual trees using the phenological subsample of trees, 1991–1996*

Species (*n* individuals)	Model	Adjusted R^2	*F*-value (df)	*P*-value
Q. lobata	Year only	0.474	27.9 (5,144)	<0.001
(25)	Flowering date only	0.002	1.3 (1,148)	0.26
	Both variables	0.485		
	Year		28.7 (5,143)	<0.001
	Flowering date		4.0 (1,143)	0.048
Q. douglasii	Year only	0.356	16.2 (5,132)	<0.001
(23)	Flowering date only	0.000	0.5 (1,136)	0.49
	Both variables	0.357		
	Year		16.2 (5,131)	<0.001
	Flowering date		1.0 (1,131)	0.31
Q. agrifolia	Year only	0.598	34.6 (5,108)	<0.001
(19)	Flowering date only	0.015	2.7 (1,112)	0.10
	Both variables	0.611		
	Year		35.4 (5,107)	<0.001
	Flowering date		4.7 (1,107)	0.033

An estimate of the overall importance of pollen limitation at both the annual and individual levels can be made by regressing acorn production of individual trees on the relative date of flowering and mean maximum April temperature across the six years of the study. Results indicate that 28.4 to 38.2 percent of the overall variance in acorn production is potentially explained by pollen limitation (*table 4*). The majority of this is due to the relatively high explanatory power of mean maximum April temperature. After controlling for this variable, pollen limitation at the individual level as indexed by date of initial flowering was only significant for *Q. agrifolia*.

Table 4—*Results of multiple regressions examining the effects of date of initial flowering (relative to the overall distribution) and mean maximum April temperature on subsequent acorn production of individual trees using the phenological subsample (N = 6 years)*

Species (*N* individuals)	Variable	R^2	*F*-value (*df*)	*t*-value	*P*-value
Q. lobata	Full model	0.309	34.3 (2,147)		<0.001
(25)	Flowering date only			1.4	0.154
	Mean max. April temp.			8.2	<0.001
Q. douglasii	Full model	0.284	28.1 (2,135)		<0.001
(23)	Flowering date only			1.0	0.33
	Mean max. April temp.			7.5	0.001
Q. agrifolia	Full model	0.382	35.9 (2,111)		<0.001
(19)	Flowering date only			2.0	0.045
	Mean max. April temp.			8.2	<0.001

Discussion

Our results support the hypothesis that pollen limitation plays a role affecting both individual and annual variation in acorn production. With respect to the former, *Q. lobata* and *Q. agrifolia* trees flowering closer to the mean date of flowering produced more acorns than those flowering either earlier or later than the peak. This is expected if pollen is limited such that trees have greater pollination success and subsequently produce more acorns if they flower when more conspecifics are flowering as well.

However, our results also suggest that the role of pollen limitation, although significant in two of the species, may be a relatively minor cause of differences in acorn productivity. Annual differences, independent of environmental variation during flowering (year), explained a far higher proportion of the variance in individual acorn production than did differences in flowering phenology.

With respect to annual variation (masting), our results are consistent with prior studies both in this population (Koenig and others 1996) and in other species in the “white oak” subgenus (Sork and others 1993; Koenig and Knops 2002) that warm, dry conditions during the spring flowering season correlate with subsequent acorn production. In our data, such conditions were considerably more important than an index of endogenous energy reserves (the prior year’s acorn crop) in predicting the subsequent mean acorn crop using the complete 23-year dataset. Because the species considered here produce mature acorns in a single year, this is consistent with pollen availability playing an important role in determining the size of the acorn crop.

Although neither the prior year’s acorn crop nor mean maximum April temperature was significantly related to mean annual acorn production in *Q. agrifolia* using the complete dataset, results with this species nonetheless suggest a significant role for pollen limitation using the six-year phenological subset of data, in which both date of initial flowering and mean maximum April temperature were significantly related to acorn production. Overall, about one-third of the total variance in acorn productivity among individuals and across years was explainable by the two variables potentially indicative of pollen limitation. In all three species, this was primarily due to the relationship between spring conditions and subsequent acorn productivity.

The significance of pollen limitation within years supports the earlier finding of Knapp and others (2001) that the number of conspecifics flowering within the vicinity of individual trees correlates with subsequent acorn production, at least in some years. Surprisingly, our support for this hypothesis did not come from *Q. douglasii* (the species studied by Knapp), but rather from the other two species studied here.

Our results also indicate that availability of locally-produced pollen may limit reproduction in some species of California oaks, and thus are consistent with data from *Q. alba* and *Q. lobata* that average pollen dispersal occurs on a very small geographic scale (Smouse and others 2001; Sork and others 2002). Such small-scale pollen dispersal implies that reproduction in oaks and possibly other wind-pollinated species may be impaired by fragmentation or other alterations to the spatial structure of their populations that reduces the availability of pollen. However, the small proportion of variation between productivity explainable by phenological differences among individuals does not preclude the possibility that considerable pollen flow occurs over much larger distances, as indicated by parentage analysis using microsatellite markers in several species (Dow and Ashley 1998a, 1998b; Streiff and others 1999). Clearly this issue deserves additional study.

In contrast, a relatively large proportion of the variance in annual acorn production by all three species appears to be due to differences in pollen availability among years correlated with environmental conditions. As with the within-year effects, the direction of the relationship implicates pollen limitation, as in all significant cases crop size was greater when conditions were more favorable for pollen flow. Primarily because of this relationship, up to 38 percent of total variance in acorn productivity is explainable by factors potentially reflecting pollen limitation. At the proximate level, this supports the hypothesis that differences in pollen availability among years plays an important role in determining annual variability in acorn production, either through fertilization or subsequent ovule development (Sork and others 1993).

What remains unclear is the ultimate cause of this pattern. A close correlation between environmental conditions favoring pollen dispersal and subsequent seed production is predicted by the hypothesis that wind pollination is an important driving force in the evolution of masting behavior, as suggested by several authors (Smith and others 1990; Satake and Iwasa 2000, 2002). However, regardless of the ultimate factors selecting for masting, trees are likely to be using some environmental cue to synchronize reproductive effort. Thus, even if masting is exclusively an adaptation to some other evolutionary challenge such as predation, a close correlation between acorn production and the environment would be predicted. The fact that this environmental variable is often one that is likely to have a strong influence on pollen flow is consistent with, but not strong evidence for, wind pollination per se being an important factor selecting for masting behavior in these species.

Regardless of the ultimate significance of the relationship between pollen availability and masting, pollen limitation appears to play at least a small role in causing differences in seed production among individuals and a larger role in producing differences in seed production among years, explaining as much as 38 percent of the overall variance in acorn productivity. Additional work is needed to clarify the spatial dimensions of pollen flow in wind-pollinated trees and clarify the role that pollen limitation plays in the evolution of masting behavior.

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A Comparative Study of Oak Seedling Physiology During Summer Drought[1]

Bruce Mahall,[2] Shelly Cole,[2] and Claudia Tyler[2]

Abstract

Over at least the last half century, rates of recruitment of young trees in California's oak woodlands have been found to be extremely uncommon, and lower than rates of mortality of mature trees for some species such as valley oak, *Quercus lobata*. This phenomenon threatens the integrity of these ecosystems. As part of a larger study of factors limiting seedling and sapling recruitment, we conducted measurements on 4 yr. old seedlings established from experimental plantings to address the questions: What effects does summer drought have on water relations, gas exchange and photosynthetic characteristics of *Q. lobata* (valley oak) and *Q. agrifolia* (coast live oak) seedlings, and how are these effects related to a successful transition from seedling to sapling life-stage? Results indicate that seedlings of both species were subject to much lower water potentials (PDXPPs) than nearby adult trees. Seedlings of *Q. lobata* had lower PDXPPs than *Q. agrifolia* seedlings. In both species, seedlings had lower maximum rates of gas exchange per unit leaf area than trees. Seedlings and trees of *Q. agrifolia* had lower gas exchange rates than seedlings and trees of *Q. lobata*. Chlorophyll fluorescence characteristics indicated leaves of seedlings and trees of both species are well protected from permanent photoinhibitory damage during summers. Variances in these physiological characteristics are being analyzed to determine relationships with seedling growth and survival.

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[2] University of California, Santa Barbara, mahall@lifesci.ucsb.edu, cole@lifesci.ucsb.edu, tyler@lifesci.ucsb.edu.

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Birds

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A Landscape Analysis of Grassland Birds in a Valley Grassland-Oak Woodland Mosaic[1]

Devii Rao,[2] Sasha Gennet,[2] Michele Hammond,[3] Peter Hopkinson,[4] and James Bartolome[5]

Abstract

While little research has been done on California grassland birds, their populations are thought to be declining due to habitat loss, fragmentation, and degradation. We investigated the association between California grassland birds and their landscape-scale habitat matrix. The habitat is a mosaic of valley grassland with blue oak and coast live oak woodlands. In this study, we used logistic regression to analyze presence of grasshopper sparrows (*Ammodramus savannarum*), horned larks (*Eremophila alpestris*), western meadowlarks (*Sturnella neglecta*), savannah sparrows (*Passerculus sandwichensis*), and the guild as a whole in response to patch size, cover-type richness, and proportion of high-intensity development, low-intensity development, deciduous forest, and evergreen forest in the landscape. These landscape variables were analyzed for the 2004 and 2005 breeding seasons at three spatial scales: 500 m, 1 km, and 2 km buffer zones from the point count center. We found that the grassland bird guild as a whole was positively associated with patch size, proportion of low-intensity development, and proportion of evergreen forest and negatively associated with cover-type richness, proportion of high-intensity development, and proportion of deciduous forest. Patch size and cover-type richness were the most commonly significant variables across spatial scales and across years. Individual species showed similar trends to that of the guild.

Keywords: California, grassland birds, habitat fragmentation, landscape analysis, patch size.

Introduction

In California, the decline of grassland bird species is thought to be associated with major changes in the grassland ecosystem (California Partners in Flight 2000). Three of the foremost ecosystem alterations in recent California history are the near complete shift from native perennial grasses to European annual species, the large-scale conversion of grassland to farmland, and continued habitat fragmentation, primarily as a result of urbanization (California Partners in Flight 2000). Ecosystem changes have led to the decline of grassland bird species not only in California but throughout the United States. This nationwide decline has been faster and more steady than that of any other guild (Knopf 1994, Peterjohn and Sauer 1999). These large shifts in population dynamics suggest that to conserve grassland birds, land managers need more in-depth and current information on how these species are

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[2] Graduate Student, Department of Environmental Science, Policy, and Management, University of California, Berkeley, CA 94720. e-mail: devii@goldridgercd.org, asgennet@nature.berkeley.edu.

[3] Staff Research Associate, Department of Environmental Science, Policy, and Management, University of California, Berkeley, CA 94720. e-mail: mhammond@nature.berkeley.edu.

[4] Post-doctoral Researcher, Department of Environmental Science, Policy, and Management, University of California, Berkeley, CA 94720. e-mail: phopkin@nature.berkeley.edu.

[5] Professor, Department of Environmental Science, Policy, and Management, University of California, Berkeley, CA 94720. e-mail: jwbart@nature.berkeley.edu.

interacting with their environment at the landscape scale. In this paper, we focus on two species known to be decreasing nationwide: grasshopper sparrow (*Ammodramus savannarum*) and western meadowlark (*Sturnella neglecta*) (Herkert 1994).

Although there are no available data on grassland birds prior to the 1800s (California Partners in Flight 2000), a general portrait of the California grassland ecosystem has emerged. Upon arrival of Europeans in North America, the first major transformation in California grasslands was from native perennial plant species to European annuals. This transformation likely began prior to the 1769 establishment of the first Spanish mission in California (Heady and others 1991, Mensing and Byrne 1998). Heady and others (1991) suggest three factors led to the conversion of the grasslands: introduction of livestock, drought, and introduction of exotic annual plant species. It was the combination of these factors working together that allowed exotic annuals to replace the native grassland vegetation. Subsequently, 75 percent of the Central Valley, which originally contained the largest area of grassland in California (Huenneke 1989), was converted to farmland by 1880 (Hewes and Gannett 1883, cited in Huenneke 1989). Today, remaining grasslands are becoming fragmented as suburbs expand, and ranch lands and farm lands are divided into smaller parcels with larger homes (California Department of Forestry and Fire Protection 2003). We propose that these factors are leading to decreasing grassland patch size available for nesting grassland birds. Therefore, managing for fragmentation provides an important opportunity for conservation of grassland bird species.

Although most grassland bird research has been done in the Midwest, researchers in California may gain insight from the results of such studies. For example, numerous publications from research in the Midwest have focused on area sensitivity: grassland birds showing preference for larger grassland patches (Herkert 1994, Vickery and others 1994, Helzer and Jelinski 1999, Winter and Faaborg 1999, Horn and others 2000, Johnson and Igl 2001, Renfrew and Ribic 2002, Bollinger and Gavin 2004, Davis 2004). Questions arising from the area sensitivity studies have led researchers to investigate the influence on grassland birds of other landscape-level factors, such as cover-type diversity, mean patch size of cover types, and amount of grassland edge (Ribic and Sample 2001, Bakker and others 2002, Fletcher and Koford 2002).

Very little research has been done on grassland birds in California. To date, studies have focused on the influence of local vegetation characteristics on grassland bird populations (Collier 1994, Goerrissen 2005, Gennet and others 2006). This paper is the first in a series of publications, in collaboration with the East Bay Regional Park District, that will take a holistic approach to grassland bird systems, looking at both landscape- and community-level factors. While there have been no studies in California to determine the influence of diminishing patch size on grassland birds, grassland fragmentation is probably exacerbating the decrease in California grassland birds (California Partners in Flight 2000). Due to this lack of information, basic data collection is needed before the proposal of any broad-scale conservation recommendations (California Partners in Flight 2000).

We aimed to quantify the effects of landscape variables on four grassland bird species: grasshopper sparrow, savannah sparrow (*Passerculus sanwichensis*), horned lark (*Eremophila alpestris*), and western meadowlark. We did this by investigating the following questions: 1. Is grassland bird presence positively associated with size of grassland patch? 2. Is grassland bird presence negatively associated with cover-type richness, in other words, number of land cover types within a specific buffer zone? 3. Is grassland bird presence negatively associated with proportion of urban development and oak woodland cover types in the landscape? The six landscape variables we analyzed were: patch size, cover-type richness, and proportion of high-intensity development, low-intensity development, deciduous forest, and evergreen forest.

Methods

Study Sites

Plots were located in seven East Bay Regional Park District properties in Alameda and Contra Costa counties (Brushy Peak, Lake Chabot, Morgan Territory, Pleasanton Ridge, Sycamore Valley, Vasco Caves, and Sunol) and in Camp Parks RFTA military installation in Dublin, California (*fig. 1*). Data were collected from 49 plots in 2004 and 62 plots in 2005. Shared characteristics of the majority of plots were large patches of valley grasslands (areas > 100 m radius) surrounded by oak woodlands and/or developed areas. The valley grassland type is primarily composed of European annual grasses, including annual ryegrass (*Lolium multiflorum*), rip-gut brome (*Bromus diandrus*), and soft chess (*Bromus hordeaceus*). The most common native species found on our plots is purple needle grass (*Nassella pulchra*, 2 percent cover), followed by: tomcat clover (*Trifolium willdenovii*), notchleaf clover (*Trifolium bifidum*), and Johnny jump-up (*Viola pedunculata*) all at 0.4 percent cover. The surrounding mosaic of oak woodland is largely made up of blue oak (*Quercus douglasii*) and coast live oak (*Quercus agrifolia*). In addition to oak woodlands, the study sites, especially Sycamore Valley and Lake Chabot, are surrounded by housing developments of differing intensity.

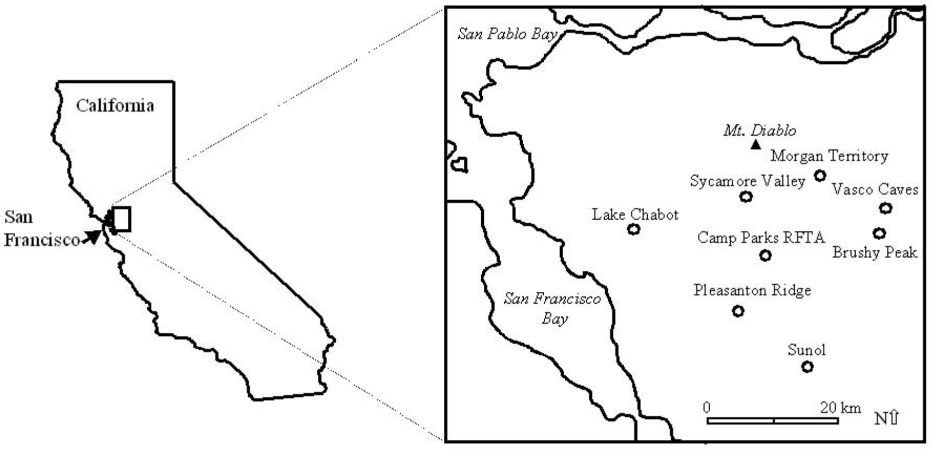

Figure 1—Study area showing East Bay Regional Park District properties and Camp Parks RFTA.

Bird Sampling

California Partners in Flight lists grasshopper sparrow, western meadowlark, and savannah sparrow as focal grassland species of conservation and management concern. We chose to study these three species in addition to the horned lark because they are dependent on grasslands for foraging and breeding.

We applied standard point count methodology for grassland bird surveys (Ralph and others 1995). Three, 10-minute point count surveys were done at each plot at least 10 days apart during the 2004 and 2005 breeding seasons. Surveys took place between March 15 and June 15. Barring high winds or inclement weather, point counts began within 15 minutes of sunrise, and the final point count of the day ended no later than four hours after sunrise. At our 100-m variable circular plots, we recorded each bird detected by sight or sound and its approximate distance to the plot center. To ensure independence among plots, point count stations were at least 200 m apart. Birds flying over the plot or detected > 100 m from the center were recorded but not used in this analysis.

Geographic Information Systems Analysis

We analyzed six landscape-level variables within three buffer zones around the plot center: 500 m, 1 km, and 2 km *(fig. 2)*. At each of these spatial scales we analyzed: 1) patch size, defined here as the total area of the grassland patch in which the point count was taken; 2) cover-type richness, defined as the total number of land cover types; 3) proportion of deciduous forest (deciduous forest is defined as areas dominated by deciduous trees); 4) proportion of evergreen forest (defined as areas with > 67 percent coniferous or broad-leaved evergreen trees); 5) proportion of low-intensity development (defined as having considerable amounts of constructed and vegetated surfaces); and 6) proportion of high-intensity development (defined as areas with high levels of constructed surfaces and little or no vegetation). To quantify these landscape variables, we used the California 2000 Land Cover Data (http://www.csc.noaa.gov/crs/lca/pacificcoast.html, last accessed August 14, 2006) created by National Oceanic and Atmospheric Administration’s Coastal Change Analysis Program. This land cover dataset was created in the year 2000, has 30 m resolution, and is projected in Albers Conical Equal Area, North American Datum 1983. We used FRAGSTATS (McGarigal and others 2002) to calculate all of the landscape variables.

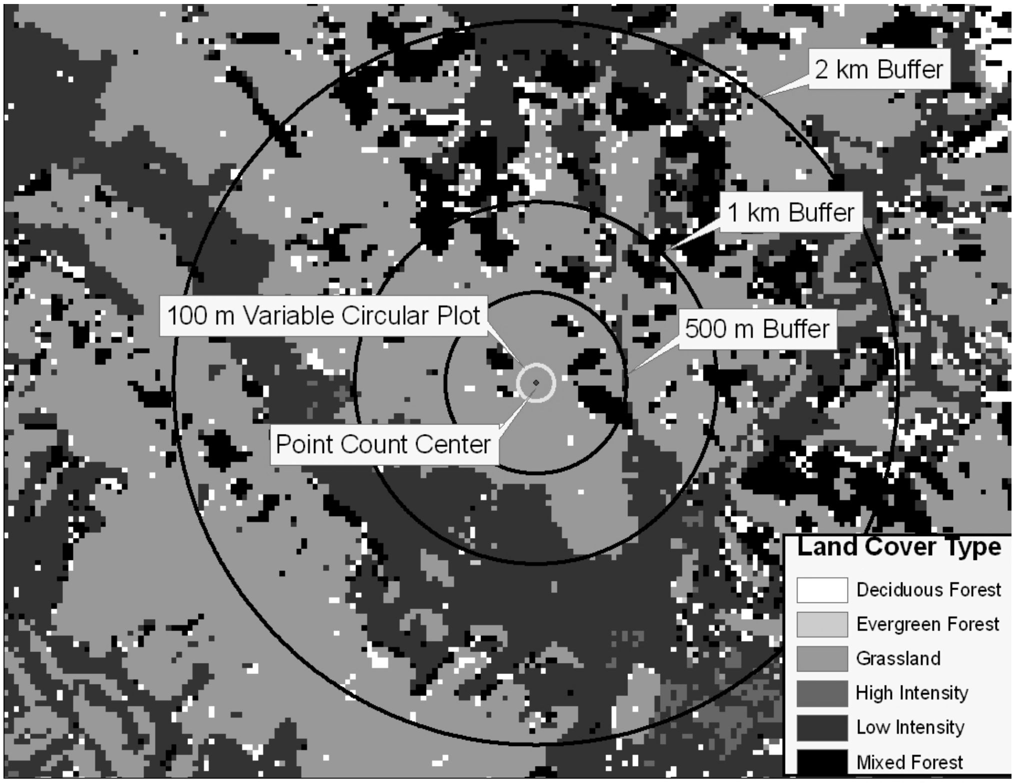

Figure 2—Land cover layer and plot layout: four concentric rings indicating extent of the plot and three buffer zones around the point count center.

Statistical Analysis

Due to the limited number of grassland bird detections, we built logistic regression models (Hosmer and Lemeshow 2000), appropriate for presence/absence data. Separate models were built for each species and for the grassland bird guild as a whole at three spatial scales and for each year. We performed backward stepwise logistic regression to generate models describing the influence of landscape scale variables on the presence of grassland birds, hand-selecting variables at each step. In each plot, a species was counted as present if it was seen at least once over the three visits per year; the guild was counted as present if any one of the four grassland bird species was detected on a plot. All six predictor variables were entered into the full model. At each step, the variable with the highest p-value was removed until only variables with a $p\text{-value} < 0.10$ remained in the model. We used $p < 0.10$ instead of the more standard $p < 0.05$ because this is a preliminary study and we did not want to exclude any important variables. The unweighted sum of squares test was used to determine the overall model fit. Final models were those with variable $p\text{-values} < 0.10$ and model fit $p\text{-values} > 0.10$. All logistic regression analyses were performed using S-PLUS 6.1. The two years of data (2004 and 2005) were analyzed separately because 13 new plots were added during the second field season.

Results

Grassland Bird Guild

The final model for the grassland bird guild, using all four species, included two variables that were consistently significant ($p < 0.10$) across both years: patch size *(fig. 3)* and cover-type richness *(fig. 4)*. In 2004, patch size was significant at 500 m and 2 km, while cover-type richness was significant at the 1 km and 2 km scales (*table 1*). In 2005, patch size entered the final model at 1 km and 2 km, while cover-type richness was significant across all three scales. The guild was also significantly associated with proportion of high-intensity development, proportion of low-intensity development, proportion of deciduous forest, and proportion of evergreen forest.

Individual Species

In both 2004 and 2005, western meadowlarks were detected on a greater number of plots than any other grassland bird species. This probably drives the similarities between results from the guild model and the individual western meadowlark species model. Like the guild as a whole, presence of western meadowlarks was associated with all six landscape variables (*table 1*). In 2004, cover-type richness was significant across all three scales. In 2005, patch size and proportion of low-intensity development were in the model at 1 km and 2 km. The only variable that was consistently significant across years for western meadowlarks was cover-type richness.

Savannah sparrows were associated with patch size, cover-type richness and proportion of evergreen forest (*table 1*). In 2004, presence of savannah sparrows was consistently associated with patch size at all three spatial scales. In 2005, cover-type richness was significant at 500 m and 1 km, and proportion of evergreen forest was significant at 500 m and 2 km. Patch size was the only variable that remained in the models for both 2004 and 2005.

Over the two years of the study, only the 2 km spatial scale in 2005 produced significant results for the horned lark (*table 1*). These significant variables were patch size, cover-type richness, proportion of deciduous forest, and proportion of evergreen forest.

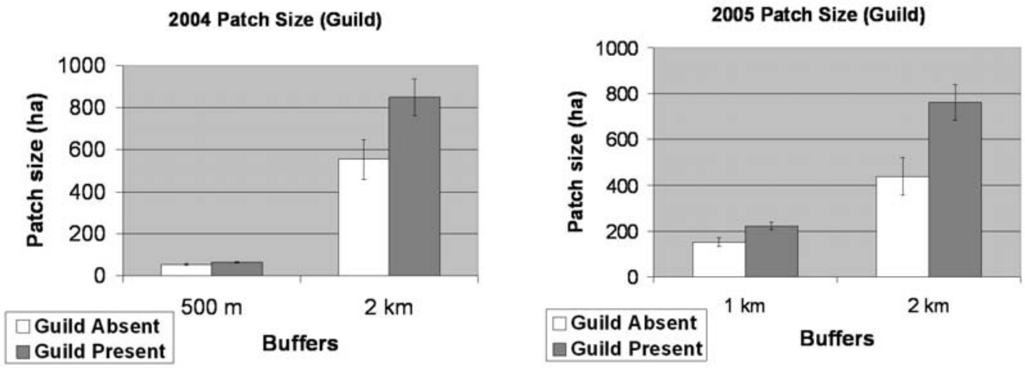

Figure 3—Mean and standard error for patch size (ha) at multiple spatial scales in plots with (shaded) and without (white) the grassland bird guild for 2004 and 2005.

Figure 4—Mean and standard error for cover-type richness (number of cover types) at multiple spatial scales in plots with (shaded) and without (white) the grassland bird guild for 2004 and 2005.

Grasshopper sparrows were detected less frequently than the other three grassland bird species in both years. Despite their rarity in our study area, grasshopper sparrow presence was significantly associated with several variables, including: cover-type richness, proportion of low-intensity development, proportion of deciduous forest, and proportion of evergreen forest (*table 1*). Proportion of deciduous forest in 2005 was the only variable that was consistently significant across spatial scales. No variables were significant in both years for grasshopper sparrows.

At the 500-m spatial scale in both years, grassland birds tended to be absent in patches that contained development. For example, grasshopper sparrows and savannah sparrows were found only in habitat matrices that did not include high-intensity development. Similarly, horned larks were found in areas with no high- or low-intensity development. Conversely, western meadowlarks were not restricted to patches without development at this scale.

Table 1—*Significant variables for the grassland bird guild and for each species individually at 500 m, 1 km and 2 km for 2004 and 2005. P-V is the p-value for the variable and P-M is the p-value for the model fit. A plus sign indicates a positive association and a minus sign indicates a negative association.*

	2004						2005					
	500 m		1 km		2 km		500 m		1 km		2 km	
Species and Variables	P-V	P-M	P-V	P-M	P-V	P-M	P-V	P-M	P-V	P-M	P-V	P-M
Guild		0.8		0.3		0.8		0.4		0.2		0.8
Patch size	+ 0.008				+ 0.04				+ 0.03		+ 0.01	
Cover-type richness			- 0.004		- 0.008		- 0.001		- 0.02		- 0.006	
% High intensity dev.	- 0.07								- 0.05			
% Low intensity dev.									+ 0.04			
% Deciduous	- 0.05											
% Evergreen forest	+ 0.04											
Western Meadowlark		0.4		0.3		0.3				0.2		0.8
Patch size									+ 0.01		+ 0.006	
Cover-type richness	- 0.003		- 0.007		- 0.01						- 0.01	
% High intensity dev.									- 0.07			
% Low intensity dev.									+ 0.05		+ 0.03	
% Deciduous forest											+ 0.098	
% Evergreen forest					- 0.06							
Savannah Sparrow		0.8		0.7		0.5		0.3		0.2		0.9
Patch size	+ 0.01		+ 0.008		+ 0.004						+ 0.01	
Cover-type richness							- 0.001		- 0.003			
% Evergreen forest							+ 0.04				+ 0.03	
Grasshopper Sparrow				0.6						0.98		0.2
Cover-type richness											- 0.098	
% Low intensity dev.											+ 0.06	
% Deciduous forest									+ 0.04		+ 0.02	
% Evergreen forest			+ 0.09									
Horned Lark												0.4
Patch size											+ 0.01	
Cover-type richness											- 0.04	
% Deciduous forest											+ 0.03	
% Evergreen forest											+ 0.06	

Discussion

Patch Size

Our results show a significant relationship between patch size and western meadowlarks, horned larks, and savannah sparrows. Western meadowlarks were found in patches ≥ 55 ha in 2004 and ≥160 ha in 2005. Savannah sparrows were found in patches ≥ 376 ha in 2004 and ≥ 124 ha in 2005. Horned larks were found in patches ≥ 124 ha in both years. Our model for grasshopper sparrows does not include patch size as a significant variable; however, they were found only in patches that were ≥ 139 ha during both study years. For both years, grassland patches in our study areas ranged from 55 to 1234 ha. Research in forest ecosystems suggests that smaller patches may cause higher rates of nest predation (Gates and Gysel 1978) and parasitism (Brittingham and Temple 1983), more interspecific competition (Ambuel and Temple 1983), and fewer appropriate breeding sites (Wilcove and others 1986).

Perhaps similar processes are occurring in grasslands. Our results agree with several studies showing that grassland birds are sensitive to patch size. For example, in Illinois, Herkert (1994) found that grasshopper sparrows only occurred in patches > 30 ha, and savannah sparrows occurred in patches > 40 ha. Grassland patch size in Herkert's study varied from 0.5 to 650 ha. In Maine, Vickery and others (1994) found that grasshopper sparrows required grassland patches of about 100 ha, whereas savannah sparrows required patches of about 10 ha. Grasslands in Vickery's study ranged from 0.3 to 404 ha. Collier (1994) found that in Southern California, grasshopper sparrow subspecies *A. s. perpallidus* had a territory size of 0.37 ± 0.16 [SD] ha. In the Midwest, grasshopper sparrows only chose breeding patches that were approximately 100 times the size of their territory (California Partners in Flight 2000). Further research may show a similar trend for California populations as well.

Cover-type Richness

At the 2 km scale, there were 14 possible cover types. Cover types fell into the following categories: grassland, forest, cultivated, developed, scrub, wetland, bare land, and water. In our study, savannah sparrows were significantly negatively associated with cover-type richness at 500 m and 1 km in 2005. Grasshopper sparrows were negatively associated with cover-type richness at the 2 km scale in 2005. Additionally, cover-type richness was in our models for the guild, western meadowlarks, and horned larks. This negative relationship between grassland bird presence and cover-type richness was expected because the more cover types in an area, the less likely grassland habitat will be available for grassland bird species. Similarly, in Wisconsin, Ribic and Sample (2001) showed that cover-type diversity, measured by the Shannon diversity index, was a key predictor of grassland bird density. They found that transects with less cover-type diversity had higher densities of grassland birds. These less diverse landscapes consisted mainly of grasslands. Savannah sparrow (at 800 m) and grasshopper sparrow (at 200 and 400 m) densities were higher in landscapes with lower cover-type diversity. Our study evaluated a similar variable using cover-type richness instead of the Shannon diversity index. We used cover-type richness because we found a multicollinear relationship between Shannon diversity index and patch size: as Shannon diversity index increased, patch size decreased. There was no multicollinear relationship between cover-type richness and patch size.

Proportion of Different Habitat Types

We analyzed proportion of deciduous forest and evergreen forest separately and found that grassland birds were most often positively associated with these variables. However, in 2004, the guild was negatively associated with deciduous forest, and western meadowlarks were negatively associated with evergreen forest. This inconsistent result is currently not understood. A negative relationship was expected between grassland birds and forested areas (oak woodlands) because the study species are dependent on grasslands for foraging and breeding, and more oak woodland in an area likely means less grassland. The generally positive association indicates, perhaps, that grassland birds require some amount of heterogeneity in their habitat at a landscape scale. Alternatively, grasslands surrounded by oak woodlands may be larger and more intact or have greater connectivity to other grassland patches than those surrounded by high-intensity development.

Studies in the Midwest have also examined proportion of different land cover types. Bakker and others (2002) analyzed proportion of woodland area at 400 m, 800 m, and 1,600 m buffers in a landscape analysis of grassland birds in South Dakota. While this variable did not enter any of their final models, they found that as the percent of woody vegetation at the grassland patch edge increased, occurrence of savannah sparrows, grasshopper sparrows, and western meadowlarks decreased. Additionally, Fletcher and Koford (2002) included proportion of woodland in the landscape in their analysis in Iowa. While their analysis included grasshopper sparrows and savannah sparrows, amount of woodland was only retained in the best model for red-winged blackbirds (*Agelaius phoeniceus*) indicating a negative relationship.

Mixed forest was another land cover type classified in our dataset that occurred in large proportions. However, there was a multicollinear relationship between mixed forest and patch size; therefore it was not used in this analysis. In the future, consideration of the proportion of mixed forest in a landscape analysis for California grassland birds may offer additional insight.

Proportion of high-intensity development was significant for the grassland guild as a whole and for western meadowlarks. The negative association with high-intensity development was expected because highly developed areas lack large grassland patches and other habitat requirements. Similarly, Bock and others (1999) evaluated edge effects at the grassland suburban interface in Colorado. Their plots were either at the suburban edge or at least 200 m from the edge. Their research showed a significant decrease in abundance of savannah sparrows and grasshopper sparrows from interior plots to the suburban edge plots. While this relationship with horned larks was not significant due to high interplot variances, they were also more often observed on interior plots. While our data cannot be directly compared to the Colorado study due to different parameters, both studies show a significant negative relationship between grassland bird populations and increased human development.

Surprisingly, the guild as a whole, western meadowlarks, and grasshopper sparrows were positively associated with proportion of low-intensity development. Low-intensity development was defined as having considerable amounts of constructed surfaces and considerable amounts of vegetated surfaces. Perhaps these species were utilizing the vegetated surfaces within the low-intensity development cover type.

Variation

Variation between buffer zones and between years is not yet clearly understood. The scope of this study was limited to landscape-scale variables which may not be adequate to explain interannual variation in species responses to their habitat. Thus, additional analysis including landscape-scale, local-scale, and environmental variables may provide a better understanding of the system. For example, grassland birds may require smaller grassland patches in heavy rainfall years, if such years produce a higher density of seeds or invertebrate prey species.

Conclusion

On our plots, California grassland birds were consistently more likely to be found in large grassland patches within a habitat matrix of few land cover types and limited development. We sampled a relatively small proportion of California grasslands, and additional research throughout the state's grasslands is needed to make broad-scale generalizations and recommendations. However, our results are consistent with research in the Midwest. Ribic and Sample (2001) noted that grassland birds respond to their landscape out to at least 800 m, Fletcher and Koford (2002) up to 1 km, and Bakker and others (2002) up to 1,600 m. Our research shows that grassland birds are responding to their habitat matrix out to at least 2 km. As urbanization continues to expand into formerly undeveloped regions, large grassland patches will shrink. We expect further research will support our assertion that in order to support California grassland bird species, land management agencies should consider purchasing unprotected lands adjacent to existing parks and other protected open space. Additionally, land trusts should build relationships with private land owners to educate and promote conservation easements. Such easements provide a flexible approach to land conservation and open space retention, allowing private land owners to continue living and working on their land. California Partners in Flight (2000) advocate protecting high-quality grassland habitat and areas that support high-grassland bird abundance. To do so, we need to define these areas by studying a broad cross-section of California's grasslands. Protection of grasslands is the first step toward conservation of grassland birds. Maintaining each grassland area will likely require site-specific management plans detailing appropriate methods for habitat enhancement.

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Continue

Breeding Season Bird Communities at Two Sierra Nevada Foothill Study Areas[1]

Barrett A. Garrison[2]

Abstract

Between late March and mid-May 2004, birds were counted during the breeding season with 10-minute point counts at 163, 100-m radius stations at two study areas on public lands in the Sierra Nevada foothills of Nevada and Yuba counties (NYC) and Tehama County (TC). Eighty-nine species of birds were detected in blue oak (*Quercus douglasii*) woodland, annual grassland, and montane hardwood habitats. Due to detection thresholds, statistical tests were done for 18 species in annual grasslands, 27 species in blue oak woodland, and 28 species in montane hardwood habitats. Habitat attributes were most similar between study areas in annual grassland and montane hardwood habitats, while blue oak woodlands in NYC had more tree cover ($P < 0.001$) and larger diameter and taller trees ($P < 0.001$). Herbaceous cover was greatest in NYC with annual grasslands ($P < 0.001$) and blue oak woodlands ($P < 0.001$). Differences in bird populations tracked habitat differences as NYC blue oak woodlands had more total average individuals and species ($P < 0.001$) and more average individuals and species ($P < 0.01$) for all six guilds. In blue oak woodlands, seven species were more numerous ($P < 0.05$) in NYC, while two species were more numerous ($P < 0.05$) in TC. Abundance estimates were equivalent between study areas for all species and guilds in annual grassland and montane hardwood habitats, except there were more shrub-nesting birds ($P < 0.01$) in NYC annual grasslands.

Keywords: Annual grasslands, birds, blue oak woodland, montane hardwoods, Nevada County, Tehama County, Yuba County.

Introduction

The Sierra Nevada foothills are one of California's most rapidly changing regions as human communities and businesses expand there. Blue oak (*Quercus douglasii*) woodland habitats are the dominant habitat in these foothills, and more than three hundred species of birds, mammals, reptiles, and amphibians are found in this habitat (Giusti and others 1996) making this habitat important for conservation. Sierra Nevada foothill habitats are being lost, degraded, and modified due to development and livestock grazing, and these habitat changes heighten concerns about conserving the foothill's wildlife resources (CalPIF 2002). In addition, there are substantial fire risks along the region's extensive wildland-urban interface further threatening these resources.

Birds are conspicuous denizens of the Sierra foothills, and birds are often studied as indicators of habitat conditions and environmental change. Residential development in California's oak woodlands does affect bird populations (Merenlender and others 1998, Strahlberg and Williams 2002), and some studies have been done on birds at scattered locations throughout the foothill region. These

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[1] An abbreviated version of the paper was presented at the Sixth California Oak Symposium: Today's Challenges, Tomorrow's Opportunities, October 9–12, 2006, Rohnert Park, California.

[2] Staff Environmental Scientist, Sacramento Valley-Central Sierra Region, California Department of Fish and Game, 1701 Nimbus Road, Rancho Cordova, CA 95670. (posthumously printed).

studies assessed impacts of livestock grazing (Verner and others 1997), residential development (Strahlberg and Williams 2002), fire regimes (Purcell and Stephens 2005), and firewood cutting (Aigner and others 1998), and investigated ecological and habitat relationships (Block 1989, Block and Morrison 1991, Purcell and Verner 1999, Verner and Purcell 1999).

Concern over the status of birds in California's oak woodlands has resulted in conservation strategies for these birds and this habitat (CalPIF 2002). There is a need, therefore, for more data on birds in this region, particularly population and community indices that can be used for some conservation purposes. This study was done, therefore, to compare bird populations on two large blocks of public lands in the Sierra Nevada foothill region where these areas are managed for multiple conservation goals. These data help establish population indices, elucidate bird-habitat relationships, and possibly identify species that are suitable for monitoring. Furthermore, these data continue to build upon an ever-increasing body of knowledge about wildlife and their habitats in the Sierra Nevada foothills.

Study Area

This study was done at two locations in Tehama County (TC) and Nevada and Yuba counties (NYC). In TC, the study area was 37,265 ha, and included the 18,965-ha Tehama Wildlife Area managed by the California Department of Fish and Game (Department), the 15,190-ha Dye Creek Preserve managed by The Nature Conservancy, and 3,110 ha from the larger Lassen National Forest managed by the U.S. Forest Service. The NYC study area totaled 7,965 ha and included the 4,635-ha Spenceville and the 1,020-ha Daugherty Hill Wildlife Areas managed by the Department, and the 2,310-ha Sierra Foothill Research and Extension Center (SFREC) managed by the University of California. The land units in TC were contiguous while the units in NYC were separated by smaller units of private lands. All areas are managed for multiple-use purposes including preserving wildlife habitat, allowing hunting, fishing, and other types of outdoor recreation, and domestic livestock grazing. In addition, research and education are primary activities at the SFREC, although these activities also occur to various degrees at the other areas.

Bird counts were done in blue oak woodlands, annual grasslands, and montane hardwood forests. Associated trees within blue oak woodlands include interior live (*Q. wislizenii*) and valley (*Q. lobata*) oaks, foothill pine (*Pinus sabiniana*), and California buckeye (*Aesculus californicus*), while shrubs included poison oak (*Toxicodendron diversilobum*), greenleaf (*Arctostaphylos patula*) and whiteleaf (*A. viscida*) manzanitas, and buckbrush (*Ceanothus cuneatus*). Non-native annual grasses and forbs such as brome (*Bromus* spp.), filaree (*Erodium* spp.), and wild oat (*Avena* spp.) dominated the herbaceous layer. Annual grassland habitat was dominated by the same grasses as blue oak woodland and had scattered individual blue and valley oaks and occasional clumps of interior live oak. In the tree layer, montane hardwood habitat was dominated by California black oak (*Q. kelloggii*) with interior live oak, California buckeye, and ponderosa pine (*P. ponderosa*) as associates, while the shrub layer had the same species as blue oak woodland. Both study areas had numerous permanent and intermittent streams as well as stock ponds for livestock watering. Spenceville Wildlife Area, in addition, had a greater number of these ponds, and it also had some food plots developed for wildlife feeding.

Elevations at the sample points were between 120 and 950 m in TC and 120 and 490 m in NYC. Because of the large size and topographic diversity of the study areas, a wide variety of slopes and aspects were found at the sample points. The topography was generally flatter in TC where most of the study area was on large flats of volcanic soils above steep canyons where Mill, Antelope, and Dye creeks flowed from east to west into the Sacramento River. These steep and largely inaccessible canyons were excluded from field work. In NYC, the topography was generally more diverse because of the numerous foothill peaks and small valleys where small creeks flowed into the Yuba River, which bisected the northern and southern halves of the study area. The TC study area is underlain by younger Cenozoic volcanic rocks, while the NYC site is underlain by older Mesozoic sedimentary and volcanic rocks that are highly metamorphosed. Annual precipitation averages are 55 cm for TC and 75 cm for NYC.

Methods

Sample Locations

Study locations were selected from a random sample of 5 percent of several thousand polygons delineated for the Sierra foothills by the Department. Polygons were generated from a geographic information system (GIS) coverage that was created by intersecting data from four biophysical attributes: precipitation, temperature, slope and aspect, and geologic substrate. From the 5 percent sample, center points of each polygon (centroid) were drawn by the GIS, and centroids were randomly chosen as study locations. Using a GIS, the centroids were visually viewed on digital orthophoto quadrangle images taken between 1998 and 2000, and centroids were randomly chosen that fell completely within the boundaries of the individual habitat units, were accessible with vehicles and/or minimal hiking, and were distributed more or less throughout the entire study area. We also selected study locations in loose groupings of two to three in the larger TC study area so that observers could minimize travel time throughout the much larger, poorly roaded, and largely inaccessible study area. With the manual selection of study locations from the initially random pool, we sacrificed some randomization of the locations in favor of logistics, access, and representativeness. Given the large number of study locations, particularly for blue oak woodlands, we were confident that the locations captured as much variation as possible in the study areas.

Equivalent numbers of study locations were initially chosen for each study area (36 in TC as follows: 4 in the Lassen National Forest; 14 in the Dye Creek Preserve; 19 in the Tehama Wildlife Area; 30 in NYC as follows: 4 in Daugherty Hill; 12 in Sierra Foothill; 14 in Spenceville) to achieve nearly equal sample sizes and survey effort, although more locations were initially needed in TC for greater coverage of the larger study area. Once field work began, five locations in TC (all from Tehama Wildlife Area) were dropped due to recent fires that denuded habitat (three locations) or the locations proved inaccessible (two locations). Dropping five locations after field reconnaissance indicated that the locations were essentially in random locations, and we were not completely knowledgeable of the ground conditions until we visited them. At each centroid, three points for bird and habitat sampling were plotted with the GIS that were 250 m apart in an equilateral triangle and centered over the initial centroids. These points were uploaded to handheld geographic positioning system (GPS) units which observers used to navigate to the points.

Bird Counts

Bird counts were done between late March and mid-May 2004 at the three points around the centroid. The count period coincided with most of the breeding season for the study areas, and bird communities consisted of yearlong, breeding, and wintering residents, as well as migrants. Counts ended in mid-May to avoid counting hatch-year birds which are harder to identify and inflate counts. The study's focus was to detect mostly adults and singing territorial males (Ralph and others 1995). The study period is referred to as the breeding season, since most of the birds bred in the study areas during this period. Birds were categorized by their residency status, based on our field observations combined with the residency information from Block (1989) and Small (1994). Birds were placed in guilds based on Zeiner and others (1990) and Verner and others (1997). Brown-headed cowbirds (*Molothrus ater*) were placed in the "Other species" guild.

Because each point was 250 m apart for spatial independence and lacked detailed on-the-ground habitat data before conducting bird counts, each point was considered a replicate. There was considerable variation in habitats around each centroid as the majority (36 of 61 [59.0 percent]) had two or more habitats at the three points. Previous bird studies in the Sierra Nevada foothills have used 150- to 300-m distances between points to ensure spatial independence (Block and Morrison 1991, Aigner and others 1998). Furthermore, standardized point count protocols (Ralph and others 1995) recommend that adjacent stations be separated by a minimum distance of 250 m. At each point, a 10-minute duration count was done once at three approximately monthly intervals between March 30 and May 15, 2004, for a total of three counts per point.

With 61 sample locations and three points per location, there were initially 183 points. After the bird counts and habitat sampling was done, 20 points were dropped from analysis because they were in habitats that had low sample sizes, including three in blue oak-foothill pine habitat, two in montane hardwood-conifer habitat, two in valley oak habitat, four in montane hardwood-conifer habitat, and nine in mixed chaparral habitat. At the 163 points used in this analysis, the three counts yielded 489 individual 10-minute duration bird counts. Bird counts began within 10 minutes of official sunrise and ended 3 to 3.5 hours later as observers visited 2 to 3 sample locations, each with 3 points, per day. With successive visits to the points, we rotated the order of the counts at the three points at each location and the order in which groups of sample locations were counted. Bird observations were limited to those occurring within a 100-m radius of the point, and laser rangefinders and flagging were used to delineate the 100-m radius boundary and verify bird distances. All birds flying over the points, heard or seen at adjacent points during counts on the same day, or were beyond the 100-m radius were eliminated from this analysis.

Six observers did the counts, and they rotated among all points to distribute observer variability as much as possible, as recommended by Ralph and others (1995). Single observers each did 103 counts (21.1 percent of the counts), 102 counts (20.9 percent), 100 counts (20.4 percent), 84 counts (17.2 percent), 76 (15.5 percent), and 24 counts (4.9 percent). All observers did approximately half their counts in each study area. Because the average number of individuals and average number of species differed ($P < 0.001$) among the five observers who did 95 percent of the counts, I combined observations from all observers given that they conducted counts in all habitats and both study areas in approximately equal proportions. All observers had normal hearing in both ears based on recent hearing tests and were trained and tested in sound and sight identification of birds from the study areas. For each habitat and study area, population measures calculated included the total number of species and total number of individuals from all species combined and for the six guilds, and the total number of individuals for each species. For each habitat and guild within each habitat, positive matching similarity indices were calculated using SYSTAT (2004) to measure commonalities in bird species composition between the study areas.

Habitat Measurements

At each point, three circular 0.10-ha (17.8-m radius) habitat plots were measured for habitat attributes. The 100-m radius point count station was subdivided into three 120° sections (1° to 120°, 121° to 240°, and 241° to 360°), and one habitat plot was placed within each section using a random compass bearing (from bearings within the section) and a random distance between 20 and 80 m so habitat plots were within the point count area. Within each habitat plot, all live trees ≥ 10 cm dbh were identified to species and measured for stem diameter at dbh. Height (m) was measured from a maximum of four live trees ≥ 10 cm closest to the habitat plot center with one tree each in four quadrants (NE, SE, SW, and NW) defined by the four cardinal compass directions. No trees were measured in the quadrant if trees were absent within the habitat plot radius.

Percent cover of live vegetation in the tree layer (> 2 m above the ground), shrub layer (0.5-2.0 m), and herbaceous layer (< 0.5 m) was measured at 25 points using a sighting tube (densitometer) held at eye level. Densitometer readings were taken at 5-m intervals along 8 transects, spaced 45° apart within the plot. Three readings each were taken on the 8 transects for a total of 24 points with the 25th point taken at the plot's center. Stem and cover data were subdivided into all trees, hardwoods only (all broad-leaved trees), and conifers only (all needled trees). Data from the three habitat plots at each bird point were averaged to describe the habitat there, and habitat types for each point were determined from these averages using the classification system of Mayer and Laudenslayer (1988).

Statistical Analysis

All statistical tests were done with SYSTAT (2004). From each bird count at each point, the total number of individuals of each species and all species combined were calculated. Totals were averaged across all three bird counts to calculate a single value for each point. Bird and habitat data for each point were then averaged from all stations within a particular habitat type. I report averages and standard errors (SE) for bird and habitat data. Comparisons of bird and habitat data between study areas within each habitat type were made with two-group *t*-tests. Results for *t*-tests with equal variances were used when variances differed by < 10 percent, while results with unequal variances were used when variances differed by ≥ 10 percent. Comparisons were made for total number of species and total number of individual birds of all species and for each guild, as well as total number of individuals for each species.

To be conservative with the analysis, birds had to be detected within a given habitat from ≥ 20 percent of the stations from one study area and ≥ 10 percent for the same habitat from the other study area for inclusion in the statistical tests. For *t*-tests with blue oak woodlands, a species had to be detected at ≥ 12 stations at the TC study area or ≥ 14 stations at the NYC study area and ≥ 6 stations at the other study area.

For *t*-tests with annual grassland and montane hardwood habitat, species had to be detected at $\geq$ 3 stations at one study area and $\geq$ 1 station at the other study area. Only species meeting detection thresholds in at least one habitat are reported in this paper[3], and data from all habitats for these species were included for completeness. Bonferroni adjustments of *P*-values for multiple comparisons were made for *t*-tests within each habitat for all birds and habitat attributes tested. Bonferroni adjustments were also made for *t*-tests within each habitat for each guild.

A one-way analysis of variance using the five observers who did almost 95 percent of the counts as the fixed effect was done to determine if differences existed among observers. Deviations from assumptions needed for parametric statistical tests were assessed using normal probability plots, measures of skewness and kurtosis, and Shapiro-Wilk tests. Logarithmic ($\log_{10}$) transformations were done to try to satisfy the statistical requirements for *t*-tests and analysis of variance for all data except the vegetation cover variables, which were given arcsine transformations (Zar 1996). Transformations improved the statistical distributions of the bird and habitat data such that parametric tests, given their robustness with medium and large sample sizes to some deviations from the required assumptions (Zar 1996), were appropriate due to the need to balance Type I (rejecting the null hypothesis of no difference between study areas when there were no differences) and Type II (not rejecting the null hypothesis when there are differences) errors. Statistical tests were considered significant when the calculated *P*-value was $\leq$ the Bonferroni-adjusted value for the basic $P \leq 0.05$.

Results

Habitat Attributes

Of the three habitat types, blue oak woodland habitats differed the most between study areas as NYC had considerably more cover ($P < 0.001$) in tree and herbaceous layers than TC (*table 1*). Although a minor component of tree cover, conifer cover was nearly 15 times greater in NYC than TC ($P < 0.001$). In NYC, mean diameters of all trees and hardwoods were 1.4 times larger ($P < 0.001$) in blue oak woodland habitat compared to TC. Trees were roughly twice as tall ($P < 0.003$) in NYC blue oak woodlands as in TC. In NYC, density and basal area of conifers in blue oak woodland habitats were three and seven times greater, respectively, than TC ($P < 0.001$), although conifers represented < 2 percent of all live trees and < 8 percent of all live tree basal area in either study area. Basal area of all trees and hardwoods were 1.7 times greater in NYC than TC ($P < 0.001$) (*table 1*). Despite larger trees, which contributed to the greater basal area in NYC, densities of all trees and hardwoods were equivalent ($P > 0.003$) in both study areas.

In annual grassland habitat in NYC, herbaceous cover was 1.7 times greater ($P < 0.001$) than TC, but no other significant differences ($P > 0.007$) were found between the two study areas for the other habitat attributes in grassland habitats (*table 1*). There were, however, some non-significant differences worth noting. In grasslands, hardwood trees had diameters two times larger ($P = 0.024$) in TC than NYC, but trees were seven times denser ($P = 0.004$) in TC than NYC. The most similar habitat was

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[3] Unpublished data for other species on file, California Department of Fish and Game, Rancho Cordova, CA.

montane hardwood habitat in which no habitat attributes differed between study areas ($P \geq 0.046$) (*table 1*).

Bird Communities and Populations

Compared to TC, there were approximately 1.4 times more bird species and individuals detected in blue oak woodland habitat in NYC ($P < 0.001$) (*table 2*). Although not statistically different ($P > 0.02$) there were considerably more species and individuals in annual grassland in NYC, while montane hardwood habitat had equivalent values ($P > 0.53$) between study areas. The percentage of detected species found in both study areas within each habitat was greatest for blue oak woodland (65.5 percent), followed by annual grassland (58.0 percent), and montane hardwood (55.2 percent) (*table 2*). Except for primary cavity nesters in annual grasslands, similarity indices within the six guilds were greatest for blue oak woodland habitat (*table 2*).

***Table 1**—Comparison of habitat attributes (mean ± standard error) between three habitats sampled for bird populations at the Tehama (TC) County, and Nevada and Yuba counties (NYC) study areas between March-May 2004.*

Habitat attribute	**Annual grassland**		**Blue oak woodland**		**Montane hardwood**	
	TC (*n* = 3-9)	NYC (*n* = 10-11)	TC (*n* = 8-58)	NYC (*n* = 13-65)	TC (*n* = 11)	NYC (*n* = 9)
Total tree cover (pct)	-[1]	-[1]	25.1 ± 1.5	46.7 ± 2.4 **[2]	46.1 ± 4.9	62.5 ± 5.6
Total hardwood cover (pct)	3.4 ± 1.1	1.9 ± 1.2	24.9 ± 1.5	43.8 ± 2.3 **	44.6 ± 4.7	59.1 ± 5.1
Total conifer cover (pct)	0	0	0.2 ± 0.1	2.9 ± 0.5 **	1.5 ± 0.8	3.4 ± 1.7
Total shrub cover (pct)	1.8 ± 0.8	0.1 ± 0.1	4.9 ± 1.5	4.0 ± 0.9	33.1 ± 8.8	15.4 ± 4.3
Total herbaceous cover (pct)	51.9 ± 2.4	89.5 ± 2.1 **[3]	57.5 ± 1.6	67.3 ± 1.9 **	41.5 ± 7.4	35.7 ± 6.2
Tree diameter (cm)	-	-	24.0 ± 0.6	33.0 ± 1.4 **	28.0 ± 1.6	25.6 ± 1.2
Hardwood diameter (cm)	27.1 ± 3.5	54.6 ± 9.1	23.9 ± 0.6	32.5 ± 1.4 **	27.2 ± 1.8	25.4 ± 1.2
Conifer diameter (cm)			42.8 ± 6.2	51.0 ± 4.1	46.5 ± 8.5	43.4 ± 7.7
Tree density (#/ha)	-	-	127 ± 10	136 ± 11	125 ± 17	179 ± 37
Hardwood density (#/ha)	21 ± 8	3 ± 2	126 ± 10	132 ± 11	121 ± 18	171 ± 37
Conifer density (#/ha)	0	0	1 ± 1	3 ± 1 **	3 ± 1	7 ± 4
Tree basal area (m^2/ha)	-	-	5.6 ± 0.3	9.3 ± 0.5 **	7.5 ± 0.9	10.0 ± 2.0
Hardwood basal area (m^2/ha)	1.2 ± 0.4	0.6 ± 0.4	5.4 ± 0.3	8.6 ± 0.5 **	6.9 ± 0.7	9.0 ± 1.7
Conifer basal area (m^2/ha)	0	0	0.1 ± 0.1	0.7 ± 0.1 **	0.6 ± 0.2	1.0 ± 0.5
Tree height (m)	-	-	6.3 ± 0.1	10.6 ± 0.3 **	10.8 ± 1.3	9.7 ± 0.7
Hardwood height (m)	6.6 ± 0.4	12.3 ± 2.0	6.3 ± 0.1	10.3 ± 0.2 **	9.5 ± 0.8	9.4 ± 0.7
Conifer height (m)	-	-	10.7 ± 1.5	21.1 ± 2.2 *	27.4 ± 7.0	22.5 ± 9.5

[1] Values for hardwoods are the same as the values for total tree cover, tree diameter, tree density, tree basal area, and tree height because all trees in annual grassland habitat were hardwoods.

[2] Results of two-group *t*-tests of $\log_{10}$ or arcsine (cover only) transformed data using Bonferroni adjusted *P*-values for 17 comparisons each within blue oak woodland (*df* = 13.9 - 121) and montane hardwood (*df* = 3.7 - 18) habitats for significance at the 0.05 level: $P \leq 0.003$ = *; $P < 0.001$ = **; no asterisks = not significant, $P > 0.003$.

[3] Results of two-group *t*-tests (*df* = 2.1 - 16.1) of $\log_{10}$ or arcsine (cover only) transformed data using Bonferroni adjusted *P*-values for 7 comparisons within annual grassland habitat for significance at the 0.05 level: $P \leq 0.007$ = *; $P < 0.001$ = **; no asterisks = not significant, $P > 0.007$.

In blue oak woodlands, 84 species were detected in both study areas, but statistical tests were done on 27 species because they met detection thresholds for this habitat (*table 2*). Seven species – the acorn woodpecker, oak titmouse, house wren, European starling, bushtit, and lesser and American goldfinches – were more abundant ($P < 0.003$) in NYC, while two species – the western meadowlark and western bluebird – were more abundant ($P < 0.001$) in TC (*table 2*). In blue oak woodland, there were greater numbers of individual birds and species ($P < 0.001$) for all six guilds in NYC.

In annual grassland habitat, 50 species were detected in both study areas, but statistical tests were done on 18 species meeting the detection threshold (*table 2*). With one exception, abundances were statistically equal ($P > 0.02$) for all measures in annual grasslands including the total number of individuals of all species combined, within each guild, and for each species. There were more shrub-nesting birds in NYC ($P < 0.001$) than TC, mostly due to the great number of red-winged blackbirds (*Agelaius phoeniceus*) in NYC (2.56 ± 1.38); no red-winged blackbirds were detected at TC annual grasslands. The total number of species as well as the total number of species for each guild were equal ($P > 0.02$) between the study areas (*table 2*).

In montane hardwood habitat, 58 species were detected in both study areas, but statistical tests were done on 28 species meeting the detection threshold (*table 2*). Abundances were statistically equal ($P > 0.008$) for all measures in montane hardwood habitat including the total number of individuals of all species combined, within each guild, and for each species. In this habitat, the total number of species as well as the total number of species for each guild were equal ($P > 0.29$) between the study areas (*table 2*).

Discussion

Bird populations differed mostly in blue oak woodland habitat, which also had the greatest differences in habitat features between study areas. In NYC, blue oak woodlands had more vegetation cover and larger trees and considerably more bird species and individuals than TC. In annual grassland habitat, NYC had more individuals and species, although not statistically significant ($P > 0.02$), and more herbaceous cover and larger trees than TC. Montane hardwood habitat was the most similar with regards to habitat attributes and bird populations. Yet, species similarity values were greatest for blue oak woodland despite the greater number of between-area habitat and bird population differences. Certainly, the larger number of count stations in blue oak woodland habitat resulted in the greater number of statistical differences in bird populations and habitat because there was greater statistical power

***Table 2** — Comparisons of the numbers (mean ± standard error) of individual birds counted with 10-minute point counts in annual grassland, blue oak woodland, and montane hardwood habitats in the Tehama County (TC), and Nevada and Yuba counties (NYC) study areas between March and May 2004*[1]

Guild Species	**Seasonal status**[2]	**Annual grassland** TC (*n* = 11)	 NYC (*n* = 9)	**Blue oak woodland** TC (*n* = 58)	 NYC (*n* = 65)	**Montane hardwood** TC (*n* = 11)	 NYC (*n* = 9)
All species							
Total individuals[3]		7.64 ± 0.86	13.11 ± 1.85	9.25 ± 0.34	13.30 ± 0.40**[4]	12.09 ± 1.21	12.59 ± 0.80
Mean species richness		4.64 ± 0.53	6.33 ± 0.58	5.93 ± 0.19	8.00 ± 0.21**	7.39 ± 0.56	8.00 ± 0.66
Species detected		35	44	64	75	45	45
Species similarity (pct)		58.0		65.5		55.2	
Ground nesters							
California quail (*Callipepla californica)*	Y	0	0.04 ± 0.04 [NT5]	0.14 ± 0.04	0.04 ± 0.04	0.58 ± 0.30	0.22 ± 0.15
Orange-crowned warbler (*Vermivora celata)*	SU	0.15 ± 0.09	0.04 ± 0.04	0.05 ± 0.02	0.18 ± 0.04	0.15 ± 0.09	0.48 ± 0.16
Lark sparrow (*Chondestes grammacus)*	Y	0.48 ± 0.12	0.59 ± 0.23	0.54 ± 0.08	0.34 ± 0.05	0.21 ± 0.10	0.07 ± 0.05
Western meadowlark (*Sturnella neglecta)*	Y	0.21 ± 0.12	0.26 ± 0.09	0.32 ± 0.06	0.08 ± 0.03**	0.15 ± 0.12	0 [NT]
Total number of individuals		1.12 ± 0.23	1.11 ± 0.27	1.36 ± 0.12	0.88 ± 0.08*[6]	1.61 ± 0.37	0.81 ± 0.27
Species richness		0.76 ± 0.13	0.70 ± 0.13	0.92 ± 0.08	0.64 ± 0.05	0.91 ± 0.16	0.67 ± 0.17
Species detected		5	6	14	14	7	4
Species similarity (pct)		37.5		55.6		37.5	
Primary cavity nesters							
Acorn woodpecker (*Melanerpes formicivorous)*	Y	0.55 ± 0.25	0.85 ± 0.28	0.89 ± 0.08	1.24 ± 0.08**	1.03 ± 0.31	1.04 ± 0.17
Nuttall's woodpecker (*Picoides nuttallii)*	Y	0.03 ± 0.03	0.11 ± 0.06	0.09 ± 0.03	0.14 ± 0.03	0.18 ± 0.07	0.07 ± 0.05
Total number of individuals		0.58 ± 0.27	1.00 ± 0.29	1.01 ± 0.09	1.43 ± 0.09**	1.27 ± 0.36	1.15 ± 0.19
Species richness		0.36 ± 0.14	0.59 ± 0.15	0.67 ± 0.04	0.90 ± 0.05**	0.73 ± 0.17	0.74 ± 0.12
Species detected		2	3	3	5	3	3

Guild Species	**Seasonal status^2**	**Annual grassland** TC (n = 11)	NYC (n = 9)	**Blue oak woodland** TC (n = 58)	NYC (n = 65)	**Montane hardwood** TC (n = 11)	NYC (n = 9)
Species similarity (pct)		66.7		60.0		50.0	
Secondary cavity nesters							
Ash-throated flycatcher (*Myiarchus cinerascens)*	SU	0.39 ± 0.10	0.30 ± 0.10	0.45 ± 0.04	0.61 ± 0.05	0.21 ± 0.09	0.44 ± 0.11
Oak titmouse (*Baeolophus inornatus)*	Y	0.61 ± 0.15	0.56 ± 0.23	1.36 ± 0.09	1.75 ± 0.09*	1.03 ± 0.23	1.59 ± 0.25
White-breasted nuthatch (*Sitta carolinensis)*	Y	0.18 ± 0.09	0.44 ± 0.17	0.33 ± 0.04	0.50 ± 0.06	0.21 ± 0.08	0.30 ± 0.10
Bewick's wren (*Thryomanes bewickii)*	Y	0.18 ± 0.10	0 ^{NT}	0.14 ± 0.04	0.18 ± 0.04	0.42 ± 0.12	0.37 ± 0.09
House wren (*Troglodytes aedon)*	SU	0	0.19 ± 0.11 ^{NT}	0.06 ± 0.02	0.23 ± 0.05**	0.15 ± 0.05	0.04 ± 0.04
Western bluebird (*Sialia mexicana)*	Y	0.36 ± 0.17	0.30 ± 0.17	0.41 ± 0.08	0.10 ± 0.03**	0.12 ± 0.09	0.07 ± 0.07 ^{NT}
European starling (*Sturnus vulgaris)*	Y	0.15 ± 0.08	0.81 ± 0.30	0.17 ± 0.04	0.56 ± 0.11**	0.18 ± 0.15	0.11 ± 0.08 ^{NT}
Total number of individuals		1.97 ± 0.25	3.30 ± 0.79	2.99 ± 0.18	4.14 ± 0.18**	2.33 ± 0.44	3.22 ± 0.26
Species richness		1.30 ± 0.17	1.85 ± 0.41	1.91 ± 0.08	2.44 ± 0.09**	1.67 ± 0.24	1.96 ± 0.21
Species detected		8	9	10	10	7	9
Species similarity (pct)		70.0		100.0		77.8	
Shrub nesters							
Western kingbird (*Tyrannus verticalis)*	SU	0.12 ± 0.07	0.70 ± 0.24	0.10 ± 0.04	0.22 ± 0.06	0.03 ± 0.03	0 ^{NT}
Western scrub-jay (*Aphelocoma californica)*	Y	0.09 ± 0.06	0.04 ± 0.04 ^{NT}	0.20 ± 0.04	0.18 ± 0.05	0.42 ± 0.09	0.19 ± 0.08
Wrentit (*Chamaea fasciata)*	Y	0.09 ± 0.09	0.04 ± 0.04 ^{NT}	0.03 ± 0.02	0.08 ± 0.02 ^{NT}	0.06 ± 0.04	0.37 ± 0.15
Wilson's warbler (*Wilsonia pusilla)*	SU	0	0.22 ± 0.10 ^{NT}	0	0.11 ± 0.03 ^{NT}	0.06 ± 0.04	0.26 ± 0.09
Spotted towhee	Y	0.06 ± 0.04	0.04 ± 0.04 ^{NT}	0.06 ± 0.02	0.21 ± 0.06	0.42 ± 0.11	0.70 ± 0.28

Guild Species	**Seasonal status[2]**	**Annual grassland** TC (*n* = 11)	NYC (*n* = 9)	**Blue oak woodland** TC (*n* = 58)	NYC (*n* = 65)	**Montane hardwood** TC (*n* = 11)	NYC (*n* = 9)
(*Pipilo maculates*)							
Total individuals		0.52 ± 0.20	3.63 ± 1.43 **	0.52 ± 0.08	1.06 ± 0.12**	1.00 ± 0.13	1.81 ± 0.47
Mean species richness		0.49 ± 0.20	1.00 ± 0.14	0.42 ± 0.06	0.70 ± 0.07*	0.91 ± 0.11	1.26 ± 0.31
Species detected		6	7	10	9	5	8
Species similarity (pct)		62.5		72.7		44.4	
Tree nesters							
Mourning dove (*Zenaida macroura*)	Y	0.09 ± 0.09	0.04 ± 0.04 ^{NT}	0.22 ± 0.05	0.14 ± 0.03	0.03 ± 0.03	0.04 ± 0.04 ^{NT}
Anna's hummingbird (*Calypte anna*)	Y	0.33 ± 0.11	0.04 ± 0.04	0.16 ± 0.03	0.16 ± 0.03	0.27 ± 0.09	0.11 ± 0.06
Bushtit (*Psaltriparus minimus*)	Y	0.09 ± 0.09	0.15 ± 0.10 ^{NT}	0.15 ± 0.05	0.88 ± 0.12**	0.36 ± 0.09	0.96 ± 0.19
Ruby-crowned kinglet (*Regulus calendula*)	WIN	0.06 ± 0.04	0.04 ± 0.04 ^{NT}	0.10 ± 0.02	0.11 ± 0.02	0.33 ± 0.10	0.11 ± 0.06
Blue-gray gnatcatcher (*Polioptila caerulea*)	SU	0	0.04 ± 0.04 ^{NT}	0.06 ± 0.02	0.14 ± 0.03	0.21 ± 0.10	0.22 ± 0.15
American robin (*Turdus migratorius*)	Y	0.21 ± 0.12	0.30 ± 0.12	0.24 ± 0.06	0.41 ± 0.05	0.85 ± 0.40	0.44 ± 0.22
Hutton's vireo (*Vireo huttoni*)	Y	0	0 ^{NT}	0.01 ± 0.01	0.13 ± 0.03 ^{NT}	0.03 ± 0.03	0.15 ± 0.06
Yellow-rumped warbler (*Dendroica coronata*)	WIN	0.67 ± 0.38	0.37 ± 0.15	0.44 ± 0.07	0.34 ± 0.06	0.85 ± 0.55	0.44 ± 0.15
Black-throated gray warbler (*Dendroica nigrescens*)	SU	0.12 ± 0.07	0.04 ± 0.04	0.03 ± 0.01	0.08 ± 0.02 ^{NT}	0.09 ± 0.05	0.04 ± 0.04
Western Tanager (*Piranga ludoviciana*)	SU	0	0.07 ± 0.07 ^{NT}	0.01 ± 0.01	0.01 ± 0.01 ^{NT}	0.09 ± 0.06	0.15 ± 0.06
Black-headed grosbeak (*Pheucticus melanocephalus*)	SU	0	0 ^{NT}	0.03 ± 0.01	0.09 ± 0.02 ^{NT}	0.12 ± 0.07	0.04 ± 0.04
Chipping sparrow (*Spizella passerine*)	SU	0	0.19 ± 0.11 ^{NT}	0.23 ± 0.05	0.31 ± 0.05	0.09 ± 0.05	0.37 ± 0.14

Guild Species	**Seasonal status**[2]	**Annual grassland**		**Blue oak woodland**		**Montane hardwood**	
		TC (*n* = 11)	NYC (*n* = 9)	TC (*n* = 58)	NYC (*n* = 65)	TC (*n* = 11)	NYC (*n* = 9)
House finch (*Carpodacus mexicanus)*	Y	0.55 ± 0.21	0.22 ± 0.10	0.26 ± 0.08	0.19 ± 0.05	0.12 ± 0.05	0.19 ± 0.10
Lesser goldfinch (*Carduelis psaltria)*	Y	1.00 ± 0.20	1.56 ± 0.41	1.22 ± 0.11	1.88 ± 0.15**	1.45 ± 0.29	1.85 ± 0.40
American goldfinch (*Carduelis tristis)*	Y	0.03 ± 0.03	0.22 ± 0.15	0.11 ± 0.03	0.34 ± 0.06**	0.45 ± 0.20	0.15 ± 0.08
Total individuals		3.45 ± 0.37	3.93 ± 0.91	3.35 ± 0.22	5.65 ± 0.28**	5.88 ± 1.23	5.56 ± 0.56
Species richness		1.73 ± 0.20	2.07 ± 0.35	1.99 ± 0.12	3.21 ± 0.15**	3.18 ± 0.38	3.33 ± 0.35
Species detected		14	17	25	34	23	20
Species similarity (pct)		63.2		63.9		59.3	
Other species							
Total individuals		0	0.15 ± 0.11 ^{NT}	0.02 ± 0.01	0.15 ± 0.03**	0	0.04 ± 0.04 ^{NT}
Mean species richness		0	0.11 ± 0.08 ^{NT}	0.02 ± 0.01	0.12 ± 0.03**	0	0.04 ± 0.04 ^{NT}
Species detected		0	2	2	3	0	1
Species similarity (pct)		0.0		25.0		0.0	

[1] Within each guild, species are listed taxonomically. Results of two-group *t*-tests (*df* = 9.3 – 120.0) of $\log_{10}$-transformed data for each species; Bonferroni adjustments made for multiple comparisons for species within each habitat (annual grassland: *n* = 18; blue oak woodland: *n* = 27; montane hardwood: *n* = 28). Species tested met the following detection thresholds: blue oak woodland: detected at ≥ 12 stations at TC or ≥ 14 stations at NYC and ≥ 6 stations at the other study area; annual grassland and montane hardwood: detected at ≥ 3 stations at one study area and ≥ 1 station at the other study area. Bonferroni-adjusted significance values for significance at the 0.05 level were: annual grasslands: $P \leq 0.003$ = *; $P < 0.001$ = **; no asterisk = not significant, $P > 0.003$; blue oak woodland and montane hardwood habitats: $P \leq 0.002$ = *; $P < 0.001$ = **; no asterisks = not significant, $P > 0.002$.

[2] Seasonal status codes: Y = yearlong resident; SU = summer resident; WIN = winter resident.

[3] Values for total individuals, mean species richness, species detected, and species similarity derived from all species detected from at least one point within each study area and habitat type.

[4] Results of two-group *t*-tests (*df* = 15.5 – 16.9) of $\log_{10}$-transformed data for total individuals and species richness; Bonferroni adjustments made for comparisons of the total number of individuals and species richness within each habitat type (*n* = 2) for significance at the 0.05 level. Significance values were: $P \leq 0.003$ = *; $P < 0.001$ = **; no asterisks = not significant, $P > 0.003$.

[5] NT = species not given *t*-tests because they did not meet detection thresholds within that habitat.

[6] Results of two-group *t*-tests (*df* = 9.9 – 118.8) of $\log_{10}$-transformed data for guilds; Bonferroni adjustments made separately for multiple comparisons for total number of individuals and species richness within each guild (*n* = 12) for significance at the 0.05 level. Significance values were: $P \leq 0.004$ = *; $P < 0.001$ = **; no asterisks = not significant, $P > 0.004$.

and a greater range of count values from the points (Aigner and others 1997, Purcell and others 2005). With more bird counting points, we might find similar differences with annual grassland and montane hardwood habitats.

The NYC study area receives greater amounts of annual precipitation and has more fertile geologic substrates, which support more vegetation cover and larger trees than TC. The younger volcanic soils in TC limit vegetation growth thereby supporting less vegetation cover and fewer and smaller trees. With greater vegetation cover and larger trees, greater bird populations should be expected in NYC. Studies of habitat relationships of birds in California oak woodland habitats found that bird populations were positively associated with vegetation cover (Block and Morrison 1991, Tietje and others 1997). In our study, total tree cover in blue oak woodland habitat was positively correlated with the total number of species ($r = 0.374$, $n = 123$, $P < 0.001$) and total number of individual birds ($r = 0.329$, $n = 123$, $P < 0.001$). In addition, there were more developed water and wildlife food plots and nearby streams in NYC which resulted in more detections of birds associated with open water and agricultural areas, although these data are not reported here[4]. Furthermore, the food plots and larger diameter and taller trees in annual grassland habitat in NYC are better habitat for European starlings (Purcell and others 2002) where it was three times more abundant than TC.

Bird populations and communities are known to differ between areas on many temporal and spatial scales (Morrison and others 1998). These between-area differences certainly represent real biological differences in which habitat conditions, demographic trends, ecological factors, and climates differ. Relationships between Sierra foothill birds and habitat features differ across the region as birds respond to the resource conditions where they reside (Block and Morrison 1991). Birds also readily respond to environmental factors that transcend simple habitat relationships (Morrison and others 1998), so variable responses among species should be expected. With the most abundant species in blue oak woodlands, there were more acorn woodpeckers, oak titmice, European starlings, bushtits, and lesser goldfinches in NYC. However, there were more western meadowlarks and western bluebirds in TC. These differences generally match the habitat preferences of these birds. Acorn woodpeckers, oak titmice, bushtits, and lesser goldfinches favor greater levels of tree cover, while western meadowlarks and western bluebirds favor open grasslands and woodlands with scattered trees (Zeiner and others 1990). At the overall population and guild levels, NYC had the greatest number of species and individuals in blue oak woodlands mostly due to habitat attributes. More detailed analysis of bird-habitat relationships for these two study areas was beyond the scope of this paper, however, future work may better elucidate these relationships.

The most abundant species in one habitat tended to be the most abundant species in the other habitats, particularly blue oak woodlands and annual grasslands. This observation supports the fact that habitats in the Sierra Nevada foothills merge together across the landscape with trees occurring to various degrees in all habitats. Furthermore, habitats were juxtaposed over small areas thereby resulting in more of a habitat mosaic than patches of distinctly different habitats. This was particularly true with blue oak woodlands and annual grasslands. With small habitat mosaics, wildlife

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[4] Unpublished data for other species on file, California Department of Fish and Game, Rancho Cordova, CA.

communities and populations should demonstrate some similarity among different habitats forming the mosaic. In addition, these birds will use several habitats, including those dominated by trees, shrubs, or grass. Management for the habitat mosaic of the Sierra Nevada foothills will certainly benefit most of these species.

Because of their abundances and associations with several foothill habitats, more abundant species would be appropriate species for monitoring. In fact, the oak titmouse, acorn woodpecker, and lark sparrow—three of the most abundant species in this study—are focus species for the California Partners in Flight oak woodland conservation effort (CalPIF 2002). Purcell and others (2005) felt that the acorn woodpecker was also a suitable candidate species of long-term monitoring because it is a keystone species and has more statistically reliable count data. At best, however, these population indices represent single-year estimates from three habitats at two locations. Statistical limitations of point count data from California oak woodlands are well known (Aigner and others 1997, Purcell and others 2005), so inferences from this study are limited. Despite the limitations, these data are baselines on bird populations and habitat characteristics from two large study areas in the Sierra Nevada foothills. The differences in bird populations between the two areas, however, must be recognized when designing and implementing conservation actions, particularly where sites are compared to each other based on wildlife populations and communities. These population indices also provide data for bird conservation efforts in California's oak woodlands (CalPIF 2002).

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Continue

Use of Hardwoods by Birds Nesting in Ponderosa Pine Forests[1]

Kathryn L. Purcell[2] and Douglas A. Drynan[2]

Abstract

We examined the use of hardwood tree species for nesting by bird species breeding in ponderosa pine (*Pinus ponderosa*) forests in the Sierra National Forest, California. From 1995 through 2002, we located 668 nests of 36 bird species nesting in trees and snags on four 60-ha study sites. Two-thirds of all species nesting in trees or snags used hardwoods for nesting, with 19 species using California black oaks (*Quercus kelloggii*) and 11 using canyon live oaks (*Quercus chrysolepsis*). Although hardwoods comprised only 17 percent of available trees, 51 percent of nests in trees were in hardwoods. The two oak species comprised more than 90 percent of the hardwoods used. Oaks used for nesting were larger than those available. Hardwood snags were seldom used. Cavity nesters used mostly conifers, especially conifer snags, but when nesting in hardwoods they nested mostly in dead portions of live trees. Of 10 species with adequate sample sizes to examine individually, six species used hardwoods more than expected [Anna's Hummingbird (*Calypte anna*), Western Wood-Pewee (*Contopus sordidulus*), Cassin's Vireo (*Vireo cassinii*), Hutton's Vireo (*Vireo huttoni*), American Robin (*Turdus migratorius*) and Black-headed Grosbeak (*Pheucticus melanocephalus*)]. Two species used conifers more than expected [Western Tanager (*Piranga ludoviciana*) and Purple Finch (*Carpodacus purpureus*)], and two species showed no overall preference compared to available trees [Hammond's flycatcher (*Empidonax hammondii*) and Steller's Jay (*Cyanocitta stelleri*)]. Western Wood-Pewees and Cassin's Vireos nested primarily in California black oaks. Hutton's Vireos, American Robins, and Black-headed Grosbeaks showed a preference for nesting in canyon live oaks. Anna's Hummingbirds used both oak species. Our results underscore the importance of hardwood trees species, particularly oaks, to birds breeding in ponderosa pine forests. For recruitment to mature trees, these shade-intolerant species need openings in the understory that were probably created primarily by fire in the past. We recommend retention of mature oaks in ponderosa pine stands, creation of openings to encourage growth of existing oaks, and management activities that encourage recruitment of oaks to replace those that die, such as carefully-applied prescribed fire.

Keywords: Breeding birds, California black oak, canyon live oak, hardwoods, nesting habitat, ponderosa pine, Quercus chrysolepsis, Quercus kelloggii.

Introduction

Hardwood forests cover more than 4.5 million hectares of land in California and are important in providing fuelwood, grazing, forest products, watershed protection, recreation opportunities, and wildlife diversity (Waddell and Barrett 2005). Hardwood forests rank among the most important for wildlife (Verner 1987). For example, more than 355 vertebrate species in the western Sierra Nevada are associated with oaks (Verner and Boss 1980). In addition to their value as a

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[2] Research Wildlife Biologist, and Wildlife Biologist, respectively, Forestry Sciences Laboratory, Sierra Nevada Research Center, Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, 2081 E. Sierra Ave., Fresno, CA 93710.

component of habitat, the propensity of hardwoods to produce large amounts of acorns at critical times of the year is a beneficial trait of these trees for wildlife (McDonald 1990, McDonald and Huber 1995).

California's hardwood resources fall into two basic groups: those that grow in the foothills and woodlands at lower elevations and those that grow in the forest zones at higher elevations (McDonald and Huber 1995). In this paper, we focus on hardwoods of forest zones of the Sierra Nevada. Hardwoods in Sierra Nevada forests are generally found as single trees or in clumps, and seldom grow in pure stands (McDonald and Huber 1995, McDonald and Tappeiner 1996). Hardwood tree species are generally shade intolerant, and require openings in the conifer canopy to sprout and grow (McDonald 1969). They are adapted to a broad range of conditions, including harsh conditions, and are able to withstand severe moisture stress (McDonald 1969, McDonald and Huber 1995, McDonald and Tappeiner 1996). Hardwoods require periodic disturbance for establishment and, with prolonged absence of disturbance, the shade-intolerant hardwoods are crowded out by conifers. (McDonald and Huber 1995, McDonald and Tappeiner 1996).

Almost 20 years ago, Verner (1987) listed critical wildlife research needs for hardwood habitats that included studying habitat preferences of wildlife associated with hardwoods, developing more accurate models of wildlife habitat relationships, and developing better models to predict successional changes in plant species composition. However, few studies to date have examined the importance of forest hardwoods to wildlife in California. Garrison and others (2005) studied the effects of group-selection harvest done to enhance stand conditions for black oak and found no adverse effects. Given the importance of hardwoods for wildlife, it is surprising that the needs of wildlife species using hardwoods have been little studied. Here we examine the use of hardwoods for nesting by birds breeding in ponderosa pine (*Pinus ponderosa*) forests in the Sierra Nevada. We examine selection for tree and snag species across all bird species and for individual species in which sample sizes allow. We also compare attributes of trees and snags used to those available for selection.

Methods

Study Areas

Four research sites were selected in ponderosa pine forests within the Sierra National Forest in the Southern Sierra Nevada, California, ranging in elevation from 1,024 to 1,372 m. Each site consisted of at least 60 ha of mature forest with relatively high canopy cover. Within the larger 60-ha plot, a 40-ha grid was established with 50 m spacing to aid in the mapping and relocation of nests. Ponderosa pine was the dominant tree species with incense cedar (*Calocedrus decurrens*) co-dominant. Other conifer species included white fir (*Abies concolor*) and sugar pine (*Pinus lambertiana*). Several hardwood species occurred in the area, the most common of which were California black oak (*Quercus kelloggii*) and canyon live oak (*Q. chrysolepsis*), but white alder (*Alnus rhombifolia*) and Oregon ash (*Fraxinus latifolia*) occurred in moist areas. Sites also included riparian elements, granitic outcrops, and shrub fields dominated by white-leaf manzanita (*Ceanothus viscida*). Portions of the study area had been impacted by past silvicultural treatments such as selective tree harvesting, however, these areas were protected from major disturbance such as timber harvest, road construction, and major fuel breaks for the duration of the study.

Fieldwork

Fieldwork began in 1995 and continued through 2002, and was part of a larger study on the productivity of forest birds across an elevational gradient (Purcell 2002). Field crews searched each 40-ha grid for nests of all bird species. Over the eight years of the study, we spent approximately 3,224 hours searching for nests on the four study sites. We recorded the substrate type (for example, tree, snag, shrub, and so forth) and plant species for each nest. We recorded height and diameter at breast height (dbh) for trees and snags. For trees, we recorded whether the portion of the tree where the nest was located was live or dead. Dbh was calculated as the sum of the diameters of all stems for multi-stemmed species rather than the geometric mean as we were interested in the overall size of the tree rather than basal area. Trees were defined as > 2 m tall. A snag was defined as having no living foliage.

To describe available trees, a total of 140 randomly-located plots were established on the four study grids. Data were recorded at 15 plots on each of the four grids in 1996, and 10 each in 1997 and 1999. Plot centers were located a random distance and direction from randomly selected points on the grid, with the stipulations that selected grid points were at least 100 m apart to avoid overlap and within 50 m of the study grid boundary. In 1996 and 1999, we recorded tree species, height, and dbh of the tree and snag closest to the plot center. In 1997, plots were divided into four quadrants and data were recorded for the nearest tree and snag in each quadrant.

Statistical Analysis

In seven cases, nests in consecutive years were built in the same location by the same species; data from only the first nest was used in analyses. We compared tree species used for nesting with available trees. We used Chi-square tests, with a continuity correction for a 2 x 2 table, to examine tree species preferences for hardwood versus conifer tree species for all nests combined, and for individual species with sample sizes of ≥ 19 nests. As is typical for this type of analysis, we examined relations between used and available trees rather than non-used trees. Although we do not know whether the trees in our available sample contained a nest, we believe the probability that available trees were used for nesting was low, as most trees were unused for nesting in any year.

Differences in tree height and dbh between nest trees and available trees were examined using *t*-tests (Proc TTEST, SAS Institute, Inc. 2004). Satterthwaite's adjustment for unequal variances was used when appropriate (Satterthwaite 1946).

Results

Over the eight years of the study, we found a total of 668 nests of 36 bird species in trees or snags in ponderosa pine forests; seven nests used in consecutive years were excluded for a total of 661 nests examined here (*tables 1 and 2*). A total of 24 of the 36 species nested in hardwood trees or snags.

Of nests in trees, 51 percent were located in hardwood tree species and hardwoods were used more than expected compared to available trees (χc2 = 79.2, P < 0.0001; fig. 1a). The two oak species comprised more than 90 percent of the hardwood species used. Nineteen species nested in California black oak trees and 11 in canyon live oak trees (*table 1*).

Hardwood snags were seldom used, although used snags did not differ from available snags (χc2 = 0.5, P = 0.47; fig. 1b). Of 151 nests found in snags, 11 percent were in hardwoods, most of which were in white alder. Species nesting in alder snags included four species of cavity nesters (Downy and Hairy woodpeckers, White-headed Woodpecker, and Red-breasted Nuthatch; see *tables 1 and 2* for scientific names) and one open nester (Pacific-slope Flycatcher). Only three nests were found in oak snags and included White-headed Woodpecker (one nest) and American Robin (two nests).

Table 1—*The number of nests found by tree species and available tree species in ponderosa pine forests in the southern Sierra Nevada, 1995 to 2002. Vertical line divides hardwood and conifer tree species.*

Bird species	California black oak	Canyon live oak	Oregon ash	White alder	Ponderosa pine	Incense cedar	Sugar pine	White fir	Total
Cooper's Hawk (*Accipiter cooperii*)	1			2	1				4
Red-tailed Hawk (*Buteo jamaicensis*)					1				1
Band-tailed Pigeon (*Patagioenas fasciata*)		1				1			2
Mourning Dove (*Zenaida macroura*)					3				3
Vaux's Swift (*Chaetura vauxi*)	1								1
Anna's Hummingbird (*Calypte anna*)	13	20		4	7	3		2	49
Acorn Woodpecker (*Melanerpes formicivorus*)					1	1			2
Downy Woodpecker (*Picoides pubescens*)	4			5					9
Hairy Woodpecker (*Picoides villosus*)	1					1			2
Northern Flicker (*Colaptes auratus*)					1				1
White-headed Woodpecker (*Picoides albolarvatus*)	1								1
Olive-sided Flycatcher (*Contopus cooperi*)					2				2
Western Wood-Pewee (*Contopus sordidulus*)	29				9	2			40
Hammond's Flycatcher[1] (*Empidonax hammondii*)	2			4	13	14			33
Pacific-slope Flycatcher (*Empidonax difficilis*)	3			4	1	2			10
Cassin's Vireo (*Vireo cassinii*)	27	12			1	19	1	2	62

Bird species	California black oak	Canyon live oak	Oregon ash	White alder	Ponderosa pine	Incense cedar	Sugar pine	White fir	Total
Hutton's Vireo (*Vireo huttoni*)	2	43				4	2	1	52
Warbling Vireo (*Vireo gilvus*)	10	2		1		2			15
Steller's Jay (*Cyanocitta stelleri*)		8			7	10		1	26
Mountain Chickadee (*Poecile gambeli*)	1				1				2
Bushtit (*Psaltriparus minimus*)	1	6							7
Red-breasted Nuthatch (*Sitta canadensis*)	1			2	1				4
Brown Creeper (*Certhia americana*)					1	3			4
Golden-crowned Kinglet (*Regulus satrapa*)						2			2
Blue-gray Gnatcatcher (*Polioptila caerulea*)	1	1			5				7
American Robin (*Turdus migratorius*)	6	21	1		11	16	1	1	57
Yellow-rumped Warbler (*Dendroica coronata*)					1	3			4
Black-throated Gray Warbler (*Dendroica nigrescens*)	3	6			5	1			15
Hermit Warbler (*Dendroica occidentalis*)					4	1		1	6
Western Tanager (*Piranga ludoviciana*)					15	4			19
Chipping Sparrow (*Spizella passerina*)					7	6		1	14
Black-headed Grosbeak (*Pheucticus melanocephalus*)	2	7		1	1	7		1	19
Purple Finch (*Carpodacus purpureus*)					25	4		2	31

Bird species	**California black oak**	**Canyon live oak**	**Oregon ash**	**White alder**	**Ponderosa pine**	**Incense cedar**	**Sugar pine**	**White fir**	**Total**
Lesser Goldfinch (*Carduelis psaltria*)					2	2			4
Total	109	127	1	23	126	108	4	12	510
Available[2]	25	15			108	84	7	2	241
Available (Summit only)[2]	8	2			25	24	2		61

[1] Hammond's Flycatchers were found on the Summit study site only.

[2] Available trees were based on plot-level vegetation measurements from all four study sites for all species, except for Hammond's Flycatcher. For Hammond's Flycatcher, tree species used for nesting were compared with available trees for the Summit study site only.

Table 2**—*The number of nests found by snag species and available snag species in ponderosa pine forests in the southern Sierra Nevada, 1995 to 2002. Vertical line divides hardwood and conifer snag species.***

Bird species	**California black oak**	**Canyon live oak**	**Oregon ash**	**White alder**	**Ponderosa pine**	**Incense cedar**	**Sugar pine**	**Unknown species**	**Total**
Northern Pygmy-owl (*Glaucidium gnoma*)					2				2
Northern Saw-whet Owl (*Aegolius acadicus*)					1				1
Acorn Woodpecker (*Melanerpes formicivorus*)					17				17
Downy Woodpecker (*Picoides pubescens*)				1					1
Hairy Woodpecker (*Picoides villosus*)				3	2	1			6
Northern Flicker (*Colaptes auratus*)					21				21
White-headed Woodpecker (*Picoides albolarvatus*)	1			1	19	1			22
Western Wood-Pewee (*Contopus sordidulus*)					1				1
Pacific-slope Flycatcher (*Empidonax difficilis*)			1	6		2		1	10
Mountain Chickadee (*Poecile gambeli*)					1				1
Red-breasted Nuthatch (*Sitta canadensis*)				1	35		2		38
Brown Creeper (*Certhia americana*)					22	1	2		25
American Robin (*Turdus migratorius*)	1	1				4			6
Total	2	1	1	12	121	9	4	1	151
Available[1]	11	2	0	2	94	59	17	8	193

[1] Available trees were based on plot-level vegetation measurements from all four study sites for all species, except for Hammond's Flycatcher. For Hammond's Flycatcher, tree species used for nesting were compared with available trees for the Summit study site only.

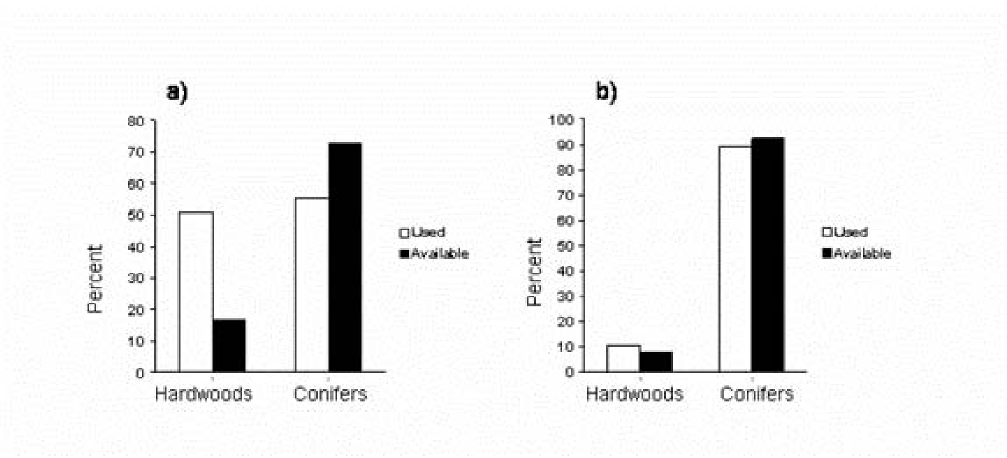

Figure 1—Proportion of hardwood and conifer trees (a) and snags (b) used as nest substrates by birds and available

More than 90 percent of nests in hardwoods were built in live portions of live trees (*table 3*). Of nests found in dead portions of live hardwood trees, the majority were cavity nests of three species: Downy Woodpecker, Red-breasted Nuthatch, and Mountain Chickadee.

***Table 3**—Numbers of nests in live hardwood trees that were found in live and dead portions of the tree in ponderosa pine forests in the southern Sierra Nevada.*

	Nests in live portion	Nests in dead portion
California black oak	96	13[1]
Canyon live oak	124	3[2]
Oregon ash	1	0
White alder	16	7[3]
Total	237	23

[1] Species included Downy Woodpecker (4 nests), Mountain Chickadee (1), Pacific-slope Flycatcher (3), Red-breasted Nuthatch (1), Western Wood-Pewee (2), Bushtit (1), and Cassin's Vireo (1).
[2] Species included American Robin (1) and Cassin's Vireo (2).
[3] Species included Downy Woodpecker (5), Pacific-slope Flycatcher (1), and Red-breasted Nuthatch (1).

Cavity nesters nested more often in conifers than in hardwoods (85 percent of nests in cavities) and 92 percent of nests in conifers were in snags. When nesting in hardwoods, however, most nests were in live trees (71 percent) and, of nests in live trees, 76 percent were in dead portions of live trees.

Oaks used for nesting were larger than those available (*table 4*). California black oak trees used for nesting averaged nearly 21 m tall, with an average total dbh of 64 cm. Canyon live oak trees used for nesting were shorter, averaging slightly more than 9 m high, but were likewise larger than available trees.

***Table 4** — Mean height and diameter at breast height (dbh) for California black oak and canyon live oak nest trees and available trees.*

	Nests Mean ± SE (*n*)	Available Mean ± SE (*n*)	*t*	df	*P*
	California black oak				
Tree height (m)	20.6 ± 0.7 (109)	16.7 ± 1.5 (26)	2.4	133	0.017
Tree dbh (cm)	64.0 ± 2.4 (109)	47.5 ± 4.4 (26)	3.1	133	0.02
	Canyon live oak				
Tree height (m)	9.3 ± 0.4 (127)	6.9 ± 0.6 (17)	3.5	37.2	0.001
Tree dbh (cm)	58.2 ± 12.0 (127)	14.5 ± 2.1 (17)	3.6	133	0.001

Of the 10 bird species for which we found ≥ 19 nests, six species used hardwoods more than expected compared to available trees and snags, two species used conifers more than expected, and two species showed no preference.

Anna's Hummingbirds showed a preference for nesting in hardwoods (χ_c^2 = 69.5, $P < 0.0001$), with 76 percent of nests in hardwoods, including 27 percent in California black oak and 41 percent in canyon live oak (*table* 1).

Western Wood-Pewees nested more often than expected in hardwood species (χ_c^2 = 52.79, $P < 0.0001$), with the overwhelming majority of nests in trees (79 percent) in California black oak (*table 1*).

Hammond's Flycatchers nested at only one site that had a greater component of mixed conifer species in a distinct riparian zone. Hammond's Flycatchers showed no preference for hardwoods vs. conifers for nesting substrates (χ_c^2 = 0.0, $P < 1.00$) compared to available trees at this site. This species, however, is a conifer specialist, with 82 percent of nests in conifers (*table 1*).

Both vireo species showed a preference for nesting in hardwoods (χ_c^2 = 52.5, $P < 0.0001$ for Cassin's Vireo, and χ_c^2 = 98.2, $P < 0.0001$ for Hutton's Vireo). Cassin's Vireos used California black oak disproportionately, with 43 percent of nests in black oak, and appeared to avoid nesting in pines (*table 1*). Hutton's Vireos nested roughly equally in trees and shrubs. Of a total of 95 Hutton's Vireo nests, 45 percent were in shrubs, all of which were whiteleaf manzanita. When nesting in trees, Hutton's Vireos showed a strong preference for canyon live oaks, with 83 percent of all tree nests in this species (*table 1*).

Steller's Jays showed no clear preference for hardwoods vs. conifers (χ_c^2 = 2.3, $P = 0.13$). Thirty-eight percent of the 26 nests were in incense cedar; 31 percent were in canyon live oak (*table 1*).

Although American Robins nested slightly more in conifers in terms of number of nests found, they preferred hardwoods as nesting substrates compared to available trees (χ_c^2 = 25.4, $P < 0.0001$). Although they were found nesting in all species of trees except white alder, 35 percent of robin nests were found in canyon live oak (*table 1*).

Western Tanagers and Purple Finches both nested only in conifers and showed a preference for conifers over hardwoods compared to available trees (χ_c^2 = 3.7, $P <$ 0.05 for Western Tanager, χ_c^2 = 4.8, $P = 0.03$ for Purple Finch; *table* 1). All of the 19 Western Tanager nests were built in two conifer species, with 79 percent in ponderosa pine. Purple Finches used ponderosa pine, incense cedar, and white fir, with 81percent in ponderosa pine.

Seventy-eight percent of Black-headed Grosbeak nests were in shrubs. When nesting in trees, they nested in hardwoods more often than expected ($\chi_c^2 = 12.5$, $P = 0.0004$), with 37 percent of nests found in both canyon live oak and incense cedar (*table 1*).

Discussion

We found that hardwoods were important as nest substrates for birds breeding in ponderosa pine forests in the southern Sierra Nevada. Hardwoods were used by 24 species—two-thirds of all species nesting in trees and snags used hardwoods to some extent. Although hardwood trees comprised only 17 percent of available trees, 51 percent of nests in trees were in hardwoods. Fifty-six percent of the 34 tree-nesting species used California black oaks; 32 percent used canyon live oaks. Six of the ten species examined individually used hardwoods more than expected, with the two oak species responsible for the observed differences.

The two oak species were used by a wide variety of bird species. Two species, Western Wood-Pewee and Cassin's Vireo, showed clear preferences for California black oak compared to available trees. Anna's Hummingbirds, Western Wood-Pewees, Cassin's Vireos, and Black-headed Grosbeaks used California black oaks for at least 25 percent of their nesting attempts. Black oaks were also preferred by Warbling Vireos nesting in ponderosa pine habitat (Purcell 2007). Studying foraging preferences of birds in mixed conifer forests, Airola and Barrett (1985) found that the insect-gleaning guild as a whole showed a preference for foraging in California black oaks compared to other tree species, with Warbling Vireos and Nashville Warblers (*Vermivora ruficapilla*) foraging more often in black oaks.

In the Sierra Nevada, California black oak grows abundantly along the west slope (McDonald 1969, 1990). Its most common associate is ponderosa pine, but white fir, incense cedar, sugar pine, and Jeffrey pine are less common associates (McDonald and Huber 1995). It will also grow on sites too poor to support ponderosa pine (McDonald 1969). In ponderosa pine forests, it is found as scattered individual trees and in small groups (Tappeiner and McDonald 1980). Due to its ability to withstand high moisture stress, black oak also grows in harsh sites too poor to support pines (McDonald 1969, 1990).

Canyon live oaks were important nest substrates for Anna's Hummingbirds, Hutton's Vireos, American Robins, and Black-headed Grosbeaks, which all used live oaks for at least 25 percent of nesting attempts. Hutton's Vireos showed a particularly clear preference for canyon live oaks (83 percent of nests in trees). They nested in both trees and shrubs, however, with 45 percent of all nests in canyon live oak, which often has a shrub-like growth form, and 45 percent in a common shrub species (whiteleaf manzanita). Live oaks are closely associated with this species, especially in California where 67 percent of reported nests were in coast live oak (*Quercus agrifolia*; Davis 1995).

Canyon live oak is widespread and is the most numerous hardwood tree species in California forest lands (Waddell and Barrett 2005). On better sites, it is shorter than its associates, and is a persistent member of the stand (McDonald and Huber 1995). On steep, rocky sites, it grows better than its associates (McDonald and Huber

1995). The shrub form grows on poor sites (McDonald and Tappeiner 1996).

While the importance of snags of coniferous tree species to wildlife is widely recognized, hardwood snags, especially oaks, were used only rarely for nesting by birds in the Sierra Nevada, including cavity-nesting species. In this study, only three nests were found in oak snags. White alder snags were the only hardwood snag species used to any degree.

Dead portions of live trees were not used by most bird species. Cavity nesters were the exception, where most nests in live trees were located in dead portions of trees where decay contributed to conditions favorable for cavity formation. Garrison and others (2002*a*) found that California black oaks had nearly three times more dead branches than ponderosa pines. They concluded that dead branches represent a significant contribution to the deadwood resource in Sierra Nevada pine-oak forests; however, they did not present any data on wildlife use. Half of the cavities used by Acorn Woodpeckers (*Melanerpes formicivorus*) were in dead limbs of live valley oaks (*Quercus lobata*; Hooge and others 1999). We found that, while dead branches were not an important nesting substrate for species that build in open cup nests, they were used by those cavity-nesting birds that used hardwoods.

Management Recommendations

The hardwood component of Sierra Nevada forests has been largely overlooked, not only in terms of commercial timber production and wood products, but for its value for wildlife, aesthetics, and water. No guidelines existed for retention of hardwoods in terms of tree size or age, basal area, canopy cover, or dispersion (Verner 1987) until the late 1980s when interim guidelines for hardwood management were developed by California Department of Fish and Game (1989) that recognized the importance of hardwood habitats to wildlife species. The 2000 Sierra Nevada Forest Plan Amendment EIS brought hardwood ecosystems to the forefront as a significant conservation issue when lower westside hardwoods were a major emphasis area (USDA Forest Service 2001).

Developing guidelines and recommendations for managing hardwood ecosystems is difficult because the plant communities of which they are a part are complex and diverse, their physical environments are variable, and the adaptations and evolutionary strategies of hardwoods are complex (McDonald and Huber 1995). Periodic disturbance of forest zone hardwoods is necessary but must be carefully considered. Without disturbance, they are out-competed by the faster-growing conifers and eventually eliminated from all but the poorest sites. In addition, managers must expand planning beyond the individual tree and stand to the landscape level, and must also acknowledge the need to consider a long timeframe for hardwood management to succeed (McDonald and Huber 1995).

Some daunting problems need to be addressed, however. Based on a multi-ownership assessment of California hardwoods and oak woodlands, the California black oak forest type had the greatest percentage decrease from 1984 to 1994 compared to other forest types (Waddell and Barrett 2005). Conifers are shading out oak seedlings and saplings, and regeneration and recruitment of young trees is insufficient to replace mortality of older trees (Garrison and others 2002*b*, McDonald and Tappeiner 1996). And, while the disease has not yet been verified in the Sierra

Nevada, California black oak and canyon live oak are susceptible to the pathogen that causes sudden oak death.

High fuel loads and fuel ladders have accumulated from decades of fire suppression. Once a hardwood stand is established, fire is undesirable because oaks are often damaged or killed by fire due to their thin bark (McDonald and Tappeiner 1996), but hardwoods require disturbance such as fire for establishment. They have the capability to sprout and grow rapidly following disturbance, and fire kills competing conifers (Tappeiner and McDonald 1980). Although fire must be used with caution in managing hardwoods, prescribed fire appears to be a viable management tool to promote seedlings and sprouts, eliminate leaf litter and destructive insects in the duff and soil, kill competing vegetation, and reduce the risk of severe stand-replacing fire (Garrison and others 2002*b*, McDonald 1990).

Large oaks were used preferentially by nesting birds. The average height of black oaks used for nesting was 21 m and was significantly larger than available black oak trees. As stated by McDonald and Huber (1995:19): “It cannot be emphasized enough that the total worth of carefully grown forest hardwoods is maximized with large trees.” Although a balance of all size and age classes is necessary, we recommend retaining large-diameter trees and creating openings around existing oaks to provide conditions for attaining large size quickly (Garrison and others 2002*b*, McDonald and Huber 1995).

There are many uncertainties surrounding the management of California forest zone hardwood ecosystems. Ecological risks will have to be taken because the high fuel loads from decades of fire suppression must be addressed. Fuels treatments can provide the periodic disturbance needed by hardwoods, but we have little information regarding how much disturbance wildlife species can tolerate without negative affects. We see reason for optimism, however, due to the growing awareness among managers of the importance of hardwood ecosystems and the need to consider hardwood resources as a priority when planning management activities.

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Continue

Reproductive Success of Oak Woodland Birds in Sonoma and Napa Counties, California[1]

Mark Reynolds,[2, 3] Thomas Gardali,[4] Matt Merrifield,[2] Robin Hirsch-Jacobsen,[4] Amon Armstrong,[4] David Wood,[2] Julia Smith,[5] Emily Heaton,[6] and Gretchen LeBuhn[3]

Abstract

Birds are often used as environmental indicators because they are conspicuous, they have a very broad constituency, respond to change at multiple spatial scales, and are sampled by standard protocols. However simple counts of birds may provide an incomplete picture of the response of bird populations to environmental change in rapidly changing landscapes like California's oak woodlands. Demographic data such as reproductive success provide a better measure of habitat quality and response to landscape modification. We collected reproductive success information on 398 nests of 38 species of birds nesting in oak woodlands of Sonoma and Napa counties in 2003 and 2004. We found no evidence that the extent of vineyard at the landscape-level had negative effects on the number of nests, frequency of nests per nest type, nor nest success. In fact, high vineyard-influence sites had slightly higher nest success. Our results suggest that remaining oak woodlands in vineyard landscapes, if properly managed and of sufficient size, can still support a diverse and productive avifauna.

Introduction

California's oak woodlands are undergoing rapid change with threats from habitat conversion and fragmentation from rural residential sprawl and vineyard development, altered fire regimes, livestock grazing, as well as sudden oak disease, and lack of regeneration (CPIF 2002, Standiford and others 2002). Developing efficient, robust biological indicators of landscape change is a challenge for conservation, especially in rapidly changing landscapes like California's oak woodlands. Birds are often used as indicators of environmental change (e.g., Carigan and Villard 2002), despite some well-founded concerns (e.g., Morrison 1986), because they are conspicuous, they have a very broad constituency, respond to environmental changes over multiple spatial scales, and standard census protocols have been developed. Studies of bird communities in California's oak woodlands highlight the ecological connections between oaks and birds through acorns, nest cavities and habitat features (Blockand others 1990, Tietje and others 1997, Verner and others 1997, Sisk and others 1997).

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[2] The Nature Conservancy, 201 Mission St. 4th floor, San Francisco, CA 94105, mreynolds@tnc.org.

[3] Department of Biology, San Francisco State University, 1600 Holloway Ave., San Francisco, CA 94132.

[4] PRBO Conservation Science, P.O. Box 1157, Bolinas, CA 94924.

[5] Holy Names University, 3500 Mountain Blvd, Oakland, CA 94619.

[6] Environmental Science, Policy and Management, University of California, Berkeley, CA 94720.

Although there are a few studies of oak woodland bird community response to habitat fragmentation (Sisk and others 1997, Merenlender and others 1998, Stralberg and Williams 2002), research on demographic effects of conversion and fragmentation of oak woodlands is lacking. To begin to fill this gap, we collected field data on 398 nests of 38 species of birds nesting in oak woodlands of Sonoma and Napa counties in 2003 and 2004, and analyzed nest number, nest type frequency, and nest success relative to the extent of vineyard conversion in the surrounding landscape.

California Oak Woodlands and Avifauna

The nine species of *Quercus* oak tree species that occur in the state contribute to forest, woodland, and savannah vegetation structural types formerly covering over 10 million acres (> 10%) of the state (FRAP 2003). Oak woodlands are thought to be the most species rich of any terrestrial habitats in the state supporting more than 330 species of vertebrates (Mayer and Laudenslayer 1988), hundreds of vascular plants and unknown numbers of invertebrate species.

Over the last 100 years, much of California’s oak woodland habitat has been converted to rangeland, agriculture, urban and sub-urban sprawl and, recently, vineyards. About two-thirds of the original extent remains, 85 percent of which is privately owned and has an uncertain future (FRAP 2003). Oak woodlands are used primarily for livestock grazing and some fuel wood-cutting, activities that are not economically sustainable in the face of development and vineyard conversion. Only 4 percent of California oak woodlands are protected at IUCN level I-III protection, making them one of the least protected of all terrestrial habitat types in the state, and consequently a focus for much conservation planning, prioritization, and protection.

A booming wine market has recently led to the rapid expansion of vineyard development in oak woodland habitats in northern and central coastal California (Merenlender 1999, 2000, Merenlender and others 2000). Much of the recent vineyard expansion has been in intact oak woodland and on hill slopes (Merenlender 2000). Acres of vineyard increased in California by 40 percent in the 10-year period from 1992 to 2002 to nearly 500,000 acres (The Wine Institute, www.wineinstitute.org). Although some vineyard development supplants other agriculture, most recent vineyard development in coastal California is occurring as conversion of woodlands and grasslands (Merenlender 2000, Heaton and Merenlender 2000).

California’s oak woodlands are intimately intertwined with their avifauna (e.g., Block and others 1990, Tietje 1990, CPIF 2002). Oak landscapes provide important habitat for birds including species that are year-round residents, summer breeders, transients, and winter migrants (Pavlick and others 1991, Tietje 1990). Some 75 species of birds regularly breed in oak habitats, one of the most diverse terrestrial avifaunas in the state (Miller 1951). Acorns are consumed by at least 30 species of birds. Three species, the Acorn Woodpecker (*Melanerpes formicivora*), Western Scrub-Jay (*Aphelocoma californica*) and Yellow-billed Magpie (*Pica nuttalli*) regularly cache acorns in the ground and thus play an active role in regeneration and range expansion of oak habitats (Carmen 1988, Koenig and Mumme 1987, Koenig 1990, Reynolds 1995). These bird species, along with the dominant oak species, are keystone species for oak woodland ecosystems in California (CPIF 2002). Recently, the bird conservation group California Partners in Flight has identified a suite of more than 20 bird species representative of California oak woodlands as “focal” species for monitoring and conservation planning (CPIF 2002, Chase and Geupel 2005), 15 of which were detected in our study area.

Methods

Study Sites

We selected study sites in Napa and Sonoma counties that were in low-elevation (below 500 m), gently sloping oak woodlands dominated by blue oak (*Quercus douglasii*) with varying degrees of surrounding habitat conversion and fragmentation, verified by aerial photographs and GIS vegetation and topographic layers. We collected nest monitoring data from six sites, two sites in 2003 and five sites (with one site sampled in both years) in 2004 (*fig. 1*).

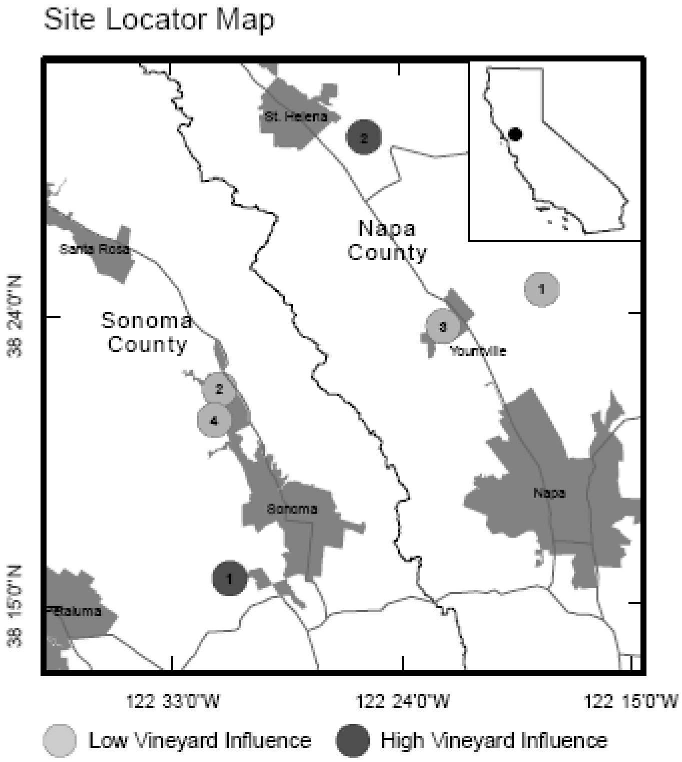

Figure 1—Location of study sites.

Extent of Vineyard Development

To determine the extent of habitat conversion and alteration around each of the six sites, we established a 1-km buffer area around the centroid of each site. Within this buffer area, we calculated the extent of habitat conversion to agricultural land uses (in ha) from the 2002 California Farmlands Mapping and Monitoring Program (California Department of Conservation 2002). The overwhelming majority of habitat conversion to agricultural land uses in this area of Napa and Sonoma counties is to vineyard. Our extent of agriculture calculations are, for comparative purposes, equivalent to the extent of vineyard development. We used these data to categorize study sites as being either "high" or "low" vineyard influence, based on the amount of agricultural conversions within a 1-km radius from the centroid of the study site. The amount of agricultural conversion with the 1-km buffer (total area of a 1-km radius circle = 314 ha) averaged 63.7 ± 74.5 (SD) ha, or 20.3 percent, agricultural conversion with values for the six individual sites of 0 (0 percent), 1.4 (0.5 percent), 19.1 (6.1 percent), 54.3 (17.3 percent), 125.6 (40 percent), and 181.6 ha (57.8 percent) of agricultural conversion. We assigned sites with greater than mean value of conversion a priori as “high” vineyard influence. Using this scheme, two sites were categorized as “high” and four were categorized as “low” vineyard influence.

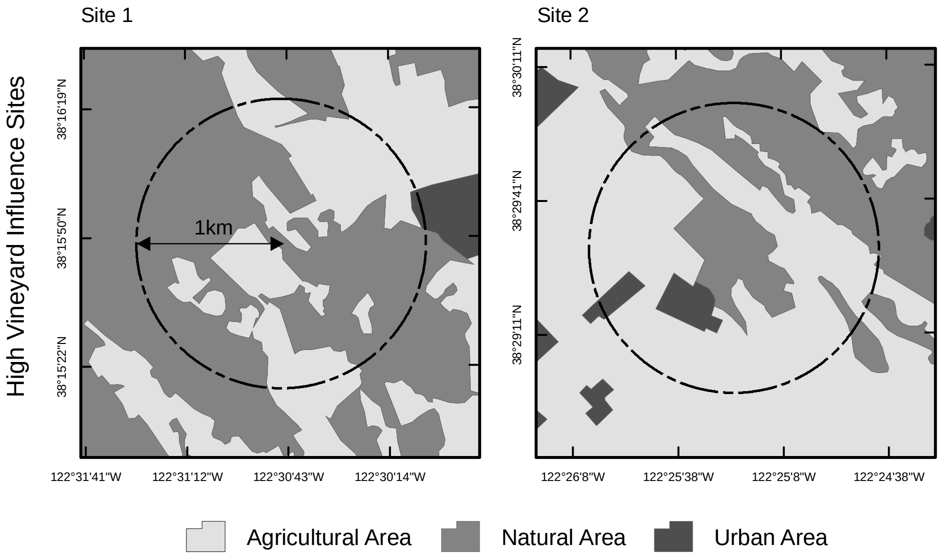

Figure 2—High vineyard influence sites.

Nest Monitoring

Nest finding and monitoring followed specific guidelines outlined by Martin and Geupel (1993). Nest finding began in mid-March and continued through mid-July. Plots were searched every two to four days, and individual nests were checked at least every four days until outcome could be determined. Much of the data was recorded based on observed parental behavior or direct visual observations. The outcome could usually be determined by timing data, conditions at the nest, or by observing fledglings near the nest.

Nests were located at all stages (construction, egg laying, incubation, and nestling stage). Nest data were recorded including observation notes, number of eggs or young, nest attempt, parental elusiveness, cue used to find nest, and a mapping description. Nests were checked carefully to minimize human disturbance. These precautionary measures included keeping visits brief, minimizing disturbance to area around nest, and staying clear of nest sites when predators were detected nearby (Martin and Geupel 1993).

Analytical Methods

We estimated daily and total survival rates using the Mayfield (1961, 1975) method. Exposure was calculated according to Mayfield’s midpoint assumption. We used non-parametric tests and ANOVA (SAS Institute 2005) to determine if nest number, frequency of nest types and nest success varied with extent of vineyard development. Because of the difficulty of interpreting unequal sampling across years, we solely used 2004 data collected at five sites to analyze the effects of extent of vineyard development and nest type on nest success.

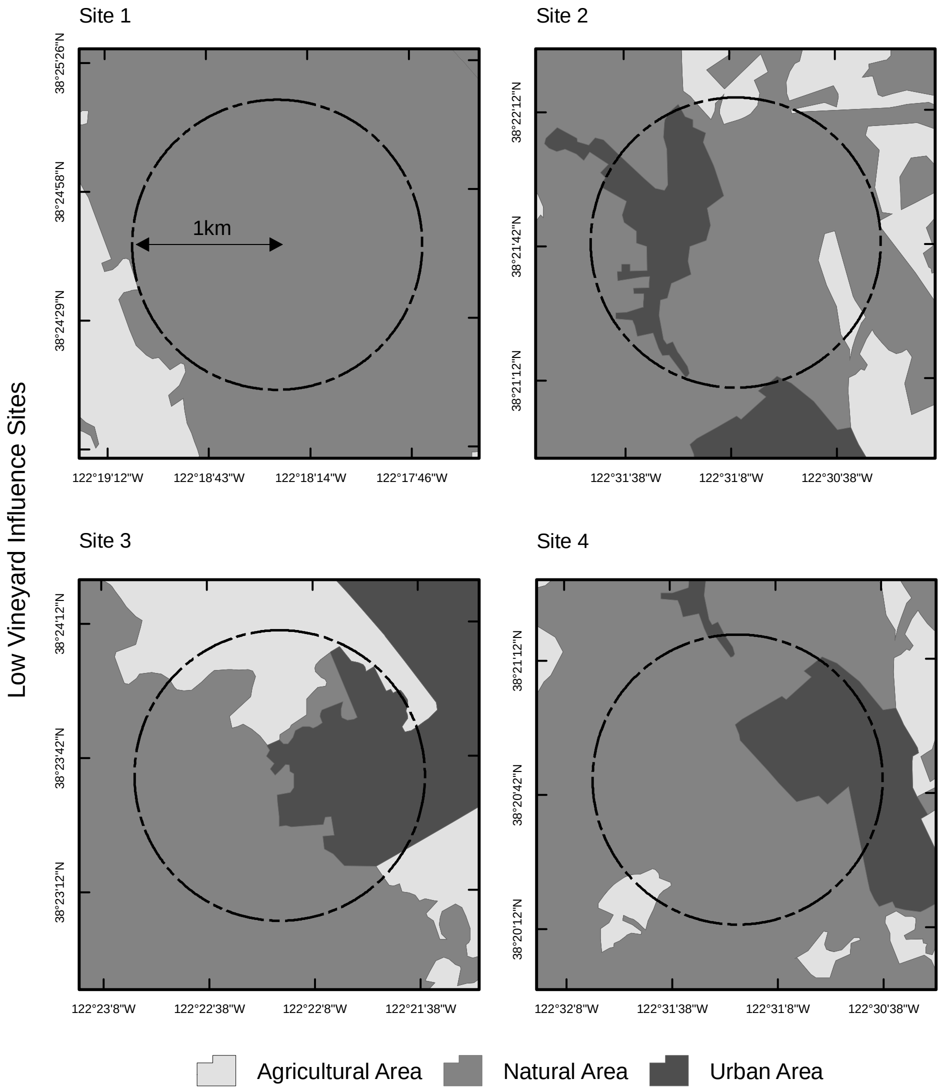

Figure 3—Low vineyard influence sites.

Results

Overall Nest Success

We monitored 398 nests of 38 species (2003: 2 sites, 240 nests, 32 species; 2004: 5 sites, 10 plots, 31 species; complete species lists and datasets are available at http://online.sfsu.edu/~lebuhn/pages/research.html). A total of 272 nests (68.3 percent) of 398 monitored were successful in producing at least one fledgling (2003: 157 of 224 nests successful = 70.9 percent; 2004: 115 of 174 nests successful = 66.1

percent). Pendulous nests (i.e., Bushtit *Psaltriparus minimus* and Bullock's Oriole *Icterus bullockii*) and cavity nests had higher overall nest success than cup or ground nests (*table 1*).

Table 1. *Total nest success by nest type 2003-04.*

Nest type	Total nests	Successful nests	% Success
Cup	135	63	0.47
Cavity	237	193	0.81
Pendulous	12	11	0.92
Ground	14	5	0.36

Daily and Total Nest Survival Probabilities

We had adequate sample sizes to calculate nest survival rates using the Mayfield (1961, 1975) method for five species (Violet-green Swallow, Oak Titmouse, House Wren, European Starling, and Dark-eyed (Oregon) Junco) including four cavity nesters (Violet-green Swallow *Tachycineta thalassina*, Oak Titmouse *Baeolophus inornatus*, House Wren *Troglodytes aedon*, and European Starling *Sturnus vulgaris*), one cup nester (Oregon Junco *Junco hyemalis*) (Oak Titmouse and European Starling are also Oak Woodland Focal Species; CPIF 2002). Daily survival probabilities for these species were all above 90 percent and total survival varied from 0.38 to 1.00 with wide and mostly overlapping 95 percent confidence intervals. Oregon Junco, a cup nesting species, had lower total nest survival than any of the other four species in 2003 (*table 2*). Oregon Junco and Oak Titmouse had lowest total survival in 2004 (*table 2*). Other species and year combinations had overlapping 95 percent confidence intervals with the exception of House Wren, for which there were no nest failures in either year (*table 2*).

Table 2. *Number of nests monitored, number of nests failed (losses), number of exposure days, and daily and total nest survival probabilities (Mayfield 1961, 1975) for species with adequate sample sizes in Sonoma and Napa counties in 2003 and 2004.*

Species	*N*	Losses	Exposure days	Daily Survival (SE)	Nesting Period	Total Survival (95%CI)
Violet-green Swallow						
2003	23	4	660	0.994 (0.003)	38.5	0.79 (0.63-0.99)
2004	21	8	489.5	0.984 (0.006)	38.5	0.53 (0.34-0.82)
Oak Titmouse						
2003	17	1	181.5	0.994 (0.006)	40.5	0.80 (0.51-1.00)
2004	18	7	203	0.966 (0.013)	27.5	0.38 (0.18-0.77)
House Wren						
2003	21	0	-	1.000	-	1.00
2004	13	0	-	1.000	-	1.00
European Starling						
2003	17	2	260.5	0.992 (0.005)	37.5	0.75 (0.50-1.00)
2004	25	3	436	0.993 (0.004)	37.5	0.77 (0.56-1.00)
Oregon Junco						
2003	23	13	163	0.920 (0.021)	27.5	0.10 (0.03-0.34)
2004	18	7	203	0.966 (0.013)	27.5	0.38 (0.18-0.77)

Effects of Vineyard Extent

We hypothesized that high vineyard extent may result in greater isolation of sites from large, intact areas of oak woodland habitat, resulting in reduced immigration and consequently nest density. We used the number of nests found and monitored at a site as a proxy for density. There was no significant effect of vineyard extent on the number of nests at a site for all nest types (*fig. 1*, Mann-Whitney *U* – test, $U = 1.5$, $p = 0.38$). We also hypothesized that high vineyard extent may alter predator and nest competitor communities with asymmetric negative effects on different nest types (e.g., greater competition for cavities, greater predation on cup nests). We found no significant effect of vineyard extent when we included the frequency of nests per nest type with number of nests at a site (*fig. 2*, ANOVA, $p > 0.05$) for cavity and cup nesters (sample sizes of ground and pendulous nesters were too small for inclusion in this analysis).

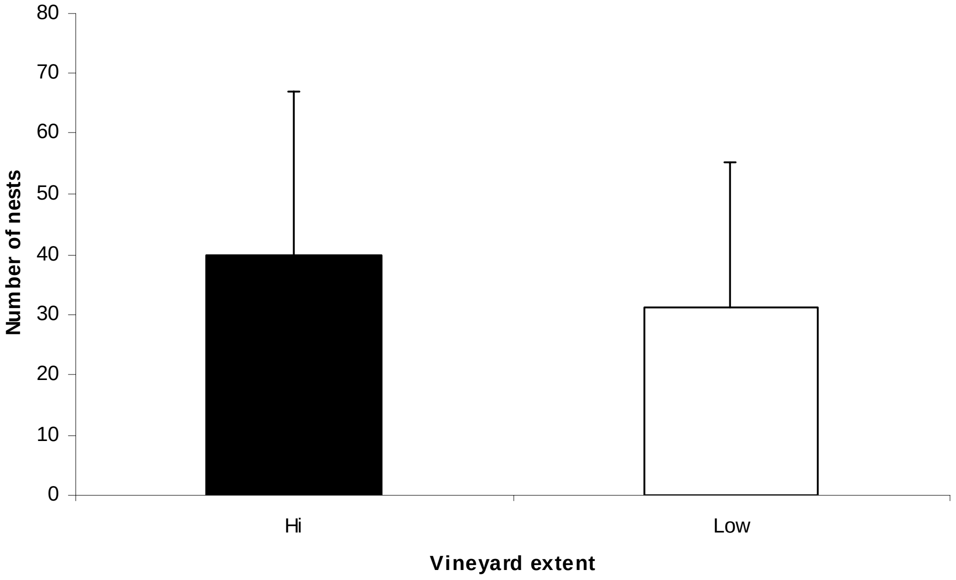

Figure 3. Effect of vineyard extent on mean (±) SD number of nests per site (Mann-Whitney *U* – test, $p > 0.05$).

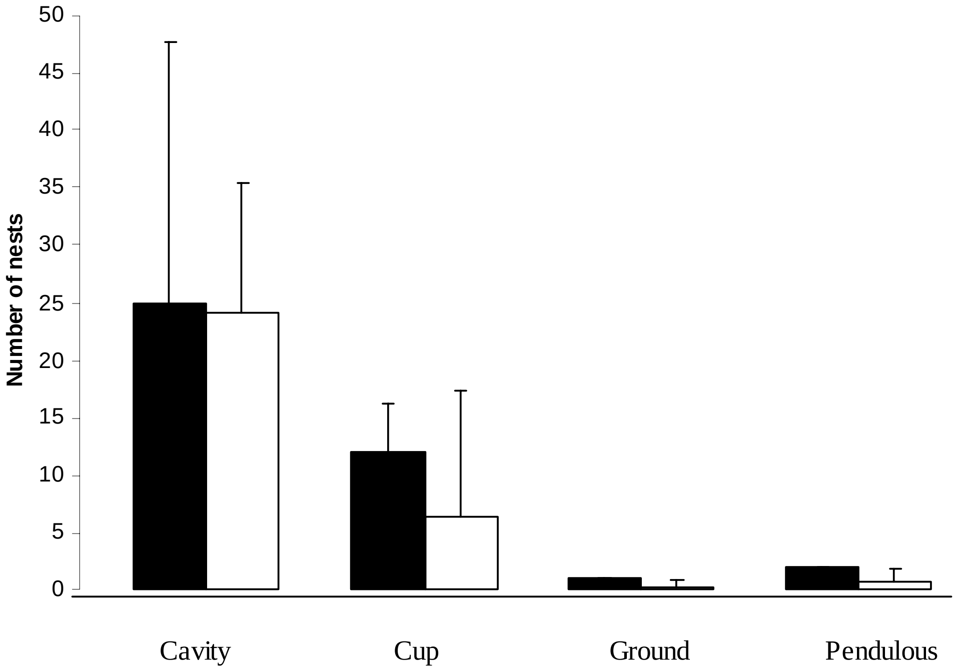

Figure 4. Mean number of nests by nest type for high (black bars) and low (open bars) vineyard extent sites ± standard deviation.

Both vineyard extent and nest type had significant effects on nest success, and there was a significant vineyard extent nest type interaction on nest success in 2004 (*table 3*). Nest success was slightly higher in sites with greater surrounding vineyard extent for all nest types (*fig. 3,* Student-Newman-Kuels post-hoc comparisons). Both cavity nests and pendulous nests had significantly higher nest success than cup nests (*fig. 3,* Student-Newman-Kuels post-hoc comparisons). To determine whether high nest success of European Starlings, which compete for nest cavities with native species, may have biased results toward higher nest success in high vineyard influence sites, we excluded them from the model with no effect on results. To determine whether higher failure rates for the small number of ground nesters ($n = 3$ nests in 2004) was biasing results we excluded ground nesters from the model. In this model, both vineyard extent and nest type were nearly significant ($p < 0.07$), but there was no significant vineyard extent-nest type interaction on nest success (vineyard extent $F = 5.4$, $p = 0.068$, nest type $F = 5.3$, $p = 0.058$, vineyard extent-nest type interaction $F = 1.4$, $p = 0.3$).

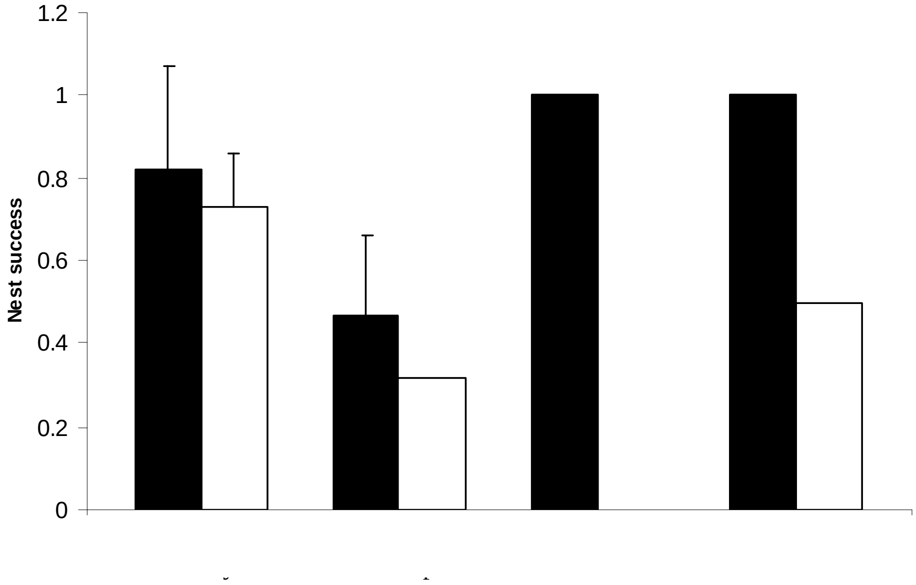

Figure 5. Mean nest success by nest type for high (black bars) and low (open bars) vineyard extent sites ± standard deviation.

Table 3. ANOVA results of effects of vineyard extent and nest type on nest success.

Variable	DF	SS	MS	F-Value	P-Value
vineyard extent	1	0.583	0.583	29.93	0.002*
nest type	3	0.368	0.123	6.30	0.028*
nest type * vineyard extent	3	0.386	0.129	6.61	0.025*
residual	6	0.117	0.020		

Discussion

The conversion of oak woodland habitat to vineyards may affect bird communities through several mechanisms, including reducing the amount of habitat, increasing the amount of habitat edge, and decreasing the quality of remaining habitat by altering predator, nest parasite, non-native cavity nesting communities, increasing nest predation and nest parasitism rates, and increasing competition for nest cavities (CPIF 2002). The magnitude of these effects is thought to depend on the scale and distribution of habitat conversion (Sisk and others 1997, Merenlender and others 1998, Stralberg and Williams 2002). Of particular concern is that remnant habitat will function as an "ecological trap" (Chasko and Gates 1982) in which remnant habitat attracts nesting birds which, because of low-habitat quality and predation, experience high nest failure.

As oak woodlands are converted and fragmented by vineyard development, we predicted that remaining oak woodland habitat would show declines in species richness and nest success. This is due to reduction of area of continuous habitat, edge effects, increased competition, and predation, particularly from increased competition from European Starlings for nest cavities and increased predation by Scrub Jays and other edge-dependent species.

Our results show that remaining oak woodlands in vineyard landscapes can still support a diverse and productive avifauna. We found no evidence that the extent of vineyard at the landscape-level had negative effects on the number of nests, frequency of nests per nest type, nor nest success. In fact, high vineyard-influence sites had slightly higher nest success. Our methods were sufficiently robust to detect differences in nest success between cavity, pendulous, and cup nesting species suggesting that we should have been able to detect landscape-level effects on nest success, if they were present, as well.

Although the negative effects of fragmentation on nest success are well known (e.g., Wilcove 1985), not all studies have shown high nest failure in fragmented habitats (e.g., Tewksbury and others 1998). The lack of any landscape-level negative effects of vineyard extent on nesting birds may have been a result of several factors, including adaptation to natural fragmentation and high ecological integrity of remaining habitat. California oak woodlands are highly heterogeneous habitats often interspersed with chaparral, bush, and patches of grassland (Griffin 1977). Many bird species nesting in oak woodlands use these other habitats for foraging and are otherwise adapted to natural levels of fragmentation and habitat heterogeneity, and will perhaps show some amount of adaptation to fragmentation by vineyards. Our sample of oak woodlands, although differing in landscape context, still contained relatively large areas of oak woodland habitat. Our sample areas may still contain areas of continuous habitat above any threshold size, as yet unknown, at which edge effects and area limitations are expressed for oak woodland bird communities. Our daily and total nest survival estimates, when compared with other published data (e.g., Flashpohler and others 2001 study of 383 nests of 8 species found total nest survival estimates between 0.36 and 0.85, compared with this study of 196 nests of 5 species with total nest survival between 0.10 and 1.0) indicate that, regardless of landscape context, these oak woodlands are very productive habitats for nesting birds. Conversely, because much of the habitat conversion associated with vineyard development in Napa and Sonoma counties is relatively recent (within the last 10 years) local extinctions of populations may not yet be detectable – a phenomenon known the “relaxation time” during which populations adjust, decline, and go extinct before reaching a new habitat-limited equilibrium (e.g., Diamond 1972, Brooks and others 1999).

Based on the predominance of total, rather than partial, nest failure, we suspected that the main cause of nest failure was predation and that the pattern of nest predation may account for the higher nest success in high vineyard-influence sites. Hilty and Merenlender (2004) show that the amount of vineyard conversion and isolation of remaining habitat patches alters the predator community from predominantly native to predominantly non-native species, including domestic cats, consistent with the “mesopredator release” hypothesis (Crooks and Soule 1999). If this is a general pattern in vineyard landscapes, perhaps nests in patches with less vineyard influence are actually subject to higher rates of predation from a more diverse native predator community.

Oak woodland bird communities have high spatial and temporal variability. Determining the effects of large-scale habitat conversion and fragmentation such as those associated with vineyard development in Napa and Sonoma counties will require large-scale and long-term monitoring and experiments. Although large, unfragmented expanses of oak woodlands should remain the highest priority for conservation, oak woodland within the vineyard matrix may have conservation value as well. If large patches of oak woodland retained within a vineyard landscape can serve as reservoirs of avian diversity and productivity, there is hope that careful conservation planning of networks of core, buffer, and connecting habitat can retain this ecologically important component of California's oak woodlands.

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Continue

Breeding Bird Assemblages in Wooded Patches in Vineyard and Undeveloped Oak Woodland Landscapes in Coastal-Central California[1]

William D. Tietje,[2] Jodi Isaacs,[2] Kata Bavrlic,[2] and Steven Rein[3]

Abstract

Widespread conversions of oak (*Quercus* spp.) woodland grassland complexes to row-crop agriculture in central coastal California have resulted in highly altered landscapes with mostly unknown consequences for faunal diversity and the health of these communities. To begin to fill this information gap, in 2002 we established study sites in vineyard and in undeveloped oak woodland-grassland landscapes in Santa Barbara and San Luis Obispo counties. In wooded patches on each of the study sites, we sampled structural elements of vegetation and surveyed breeding bird point count stations. We summarized the data by 95 percent CI. Row crops, mostly vineyards, comprised two-thirds of the vineyard landscape, compared to two-thirds woodland in the oak woodland-grassland landscapes. With the exceptions of duff and canopy cover, vegetative attributes were similar in the wooded patches on both landscapes. Breeding bird assemblages were also similar in the two landscapes. Of the 10 most detected bird species, nine were common to both landscapes. Of the six species unique to vineyard landscape, three are species that the literature usually describes as adapted to open habitats. In the oak woodland-grassland landscapes, three of the five unique species we recorded may be sensitive to fragmentation. The concepts of patch size, isolation, and source-sink dynamics should be considered in a longer-term study before these preliminary results are used as an indication that native avifauna can persist in small, isolated treed patches in highly altered landscapes.

Keywords: Bird abundance, bird diversity, California oak woodland, habitat management, land use, landscape ecology.

Introduction

Vineyards expanded rapidly the past two decades in north- and central-coastal counties of California (U.S. Department of Agriculture/Weights and Measures 2001, Merenlender 2000), often resulting in a mosaic of small residual wooded patches surrounded by open agricultural development and associated roads and support facilities. Wildlife biologists, resource managers, planners, and agriculturists wonder about habitat fragmentation and possible loss of biodiversity in these developed landscapes. They ask, "to what extent do woodland fragments provide usable foraging, roosting, and nesting habitat for wildlife . . . to what extent do they retain and contribute to the maintenance of wildlife diversity?"

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[1] An abbreviated version of this paper was presented at the Sixth California Oak Symposium: Today's Challenges, Tomorrow's Opportunities October 9-12, 2006, Rohnert Park, California.

[2] Department of Environmental Science, Policy, and Management, University of California, Berkeley, CA 94720.

[3] Statistics Department, California Polytechnic State University, San Luis Obispo, CA 93407.

To date, no study has assessed avifaunal assemblages in residual wooded patches surrounded by row crops, compared to avifaunal assemblages in undeveloped California oak woodland. Little scientific basis therefore exists to guide growers and local planning agencies. This paper presents preliminary results on natural vs. induced habitat fragmentation on California oak woodland avifauna.

Study Areas

Study Area Selection

To study bird assemblages in residual patches (vineyard landscape) and undeveloped oak woodland (oak woodland-grassland landscape), we used geographic information systems (GIS) to divide the Los Berros area east of Nipomo in southwest San Luis Obispo County and part of the Santa Ynez Valley in Santa Barbara County, into levels of vineyardization (Merenlender and Heaton, unpublished data). The algorithm treats the counties as a grid composed of 25 m^2 cells. It calculates the level of vineyardization as a function of the amount and distribution of vineyard landscape (mostly vineyards) within 2,000 m of each cell and averages the values for all cells. The algorithm produced a map with “contour” lines indicating varying degrees of vineyardization of the landscape expressed as percent vineyardization values. Using this map, we then selected two vineyard landscape (treatment) and two oak woodland-grassland landscape (control) study areas—one in San Luis Obispo County and three others in Santa Barbara County (*fig. 1*).

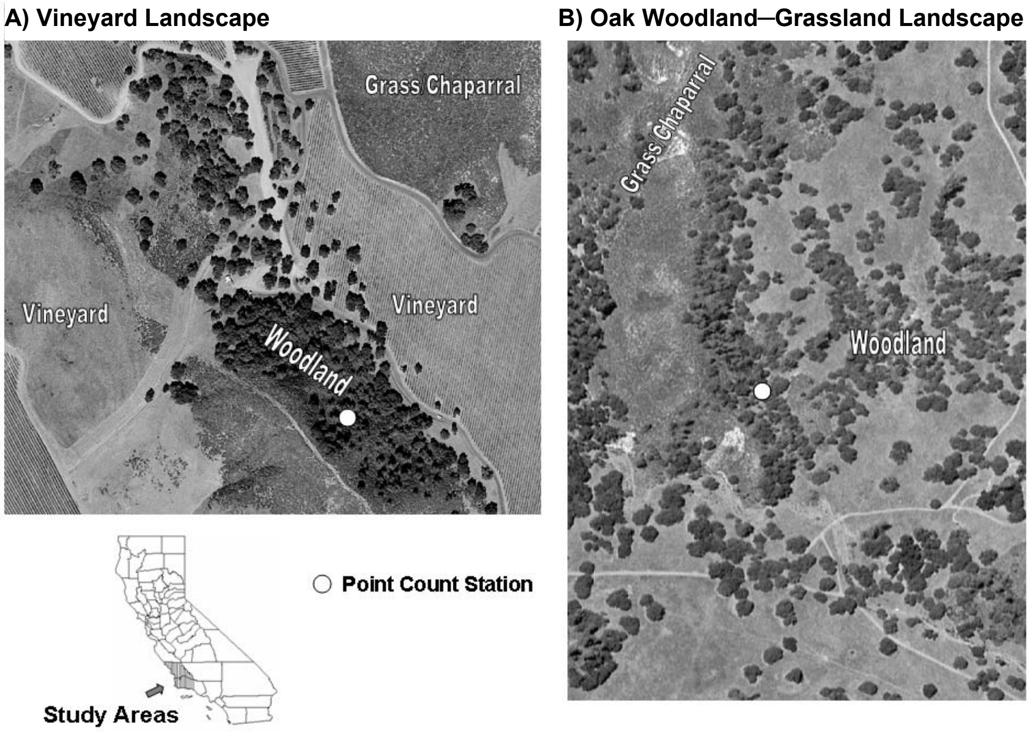
Study Site Characteristics

All study sites are within the coast live oak phase (Griffin 1988) of the central coast ranges. Coast live oak (*Quercus agrifolia*) predominates in the overstory, interrupted occasionally with a blue oak (*Q. douglasii*) or valley oak (*Q. lobata*) tree. When present, the understory is composed of poison oak (*Toxicodendron diversilobum*), toyon (*Heteromeles arbutifolia*), redberry (*Rhamnus crocea*), and ceanothus (*Ceanothus* spp.). On the woodland floor, wild oats (*Avena* spp.), bromes (*Bromus* spp.), and fescues (*Festuca* spp.) dominate. Common forbs include deerweed (*Lotus scoparius*), fiddleneck (*Amsinckia* spp), filaree (*Erodium* spp.), and hummingbird sage (*Salvia spathacea*). Woodland patches in the vineyard landscape average 5 to 20 ha and usually occur in areas where the hilly topography limits row crop agriculture. Wooded patches on the oak woodland-grassland landscape study areas are also more prevalent on the east- and north-facing hillsides, a general characteristic of California coastal oak woodland.

Methods

Bird Point Counts

Using a 250-m scaled grid overlaid on a digital map of the study areas, we randomly selected 15 points, each entirely within a woodland patch in each of the two vineyard landscape and oak woodland-grassland landscape study sites (total of 60 points). From 23 April to 26 June 2002, we surveyed birds within 50-m radius plots centered on the points four times during sunrise to 1000 PST, systematically rotating station visits among observers by study site, count station, and time of day (Bibby and others 2000, Ralph and others 1995). We recorded the species and number of birds detected during the timed counts.


A) Vineyard Landscape

B) Oak Woodland–Grassland Landscape

Figure 1—Map showing examples of the land matrices used for the Vineyard Landscape and Oak Woodland-Grassland Landscape study sites in San Luis Obispo and Santa Barbara counties. The Vineyard Landscape study sites (A) were chosen in woodland areas where row cropping, mostly vineyards, predominated. The Oak Woodland-Grassland Landscape study sites (B) were selected in undeveloped Oak Woodland-Grassland Landscape.

Landscape-level Vegetation Coverage

To calculate landscape-level vegetative cover, we placed a 100-m grid over a GIS map of each study area and counted the grid intersections that occurred in treed patches, grass/chaparral, cropped, and human development (e.g., roads, buildings, water developments). Approximately 1,600 intersections per each of the four study sites were adequate to determine percent cover of each vegetation type.

Patch-level Vegetation Sampling

In summer 2006, we randomly chose 24 of the 60 count stations (6 at each site) for stand- or patch-level vegetation sampling. Because of change of ownership at one of the oak woodland-grassland landscape sites, we conducted the vegetation sampling in woodland of similar vegetation composition and structure on an adjacent property. At 10 m from the sample point in the four cardinal directions (N, S, E, W), we used a 1-m^2 frame to visually estimate percent ground cover (grass/forbs and duff), a density pole (Griffith and Youtie 1988) to measure understory obstruction (an index of shrub cover), and a concave spherical densiometer (Lemmon 1956) to measure canopy cover. As an index of tree density, we measured the distance from the sampling point to the nearest tree ≥10 cm dbh and ≥1.5 m tall in each of four quadrants (NE, SE, SW, NW) centered on the sampling point. We also recorded the species and diameter breast height (DBH) of these trees. Finally, within 10 m of each sample point, we counted pieces of coarse woody debris (CWD) ≥10.2 cm diameter and ≥1.0 m long with ≥30 cm in contact with the ground.

Data Analyses

Because there were only two replicates per treatment in this study, we chose to report 95 percent CI for the mean differences in vegetation structure and between oak woodland-grassland landscape and vineyard landscape areas, rather than conduct inferential statistics. Although bird monitoring data was adequate for inferential statistics, replication was still low. Therefore, we also calculated means and SE for the number individuals of species for each point count over the four visits and two replications. Because most bird detections in oak woodland are auditory rather than by sight (Block 1989), and to limit the inflationary effects on the surveys of flocking, we also indexed bird abundances on the vineyard landscape and oak woodland-grassland landscape sites by the percent of visits at which a species was detected. Hence, we calculated the percents of 120 station visits (15 stations on each of the two sites × 4 visits per station = 120) in oak woodland-grassland landscape and 120 visits in vineyard landscape in which the species was detected.

Results

Vegetation

Landscape Matrix

The oak woodland-grassland landscape was dominated by treed patches (65 percent). In contrast, row-crops (62 percent) dominated the vineyard landscape study areas (*table 1, fig. 1*). Tree cover, mostly in small (<20 ha), isolated patches, comprised only 15 percent of the vineyard landscape study sites. Grass/chaparral vegetation occurred over approximately a quarter of both study sites (35 and 22 percent, respectively). Buildings for machinery, irrigation ponds, dirt- or gravel-based roads, and other infrastructure for row-crop agriculture comprised <1 percent of the cropped areas. We did not detect these facilities on the oak woodland-grassland landscape.

Table 1—*Percent vegetation cover types on the vineyard landscape and oak woodland-grassland landscape study sites***.**

	Vineyard Landscape	Oak Woodland-Grassland Landscape
Treed patches	15%	65%
Row crops	62%	
Grass/chaparral	22%	35%
Human development	1%	

Patch-level Structure

Coast live oak predominated in the woodlands (100 percent of trees tallied) on oak woodland-grassland landscape and in vineyard landscape (98 percent of trees tallied).

With the exceptions of duff and tree canopy covers, all of the habitat elements measured (grass/forbs, shrub cover, tree distance [index of tree density], Tree DBH, and CWD) were similar in the wooded patches of both landscapes (*fig. 2*).

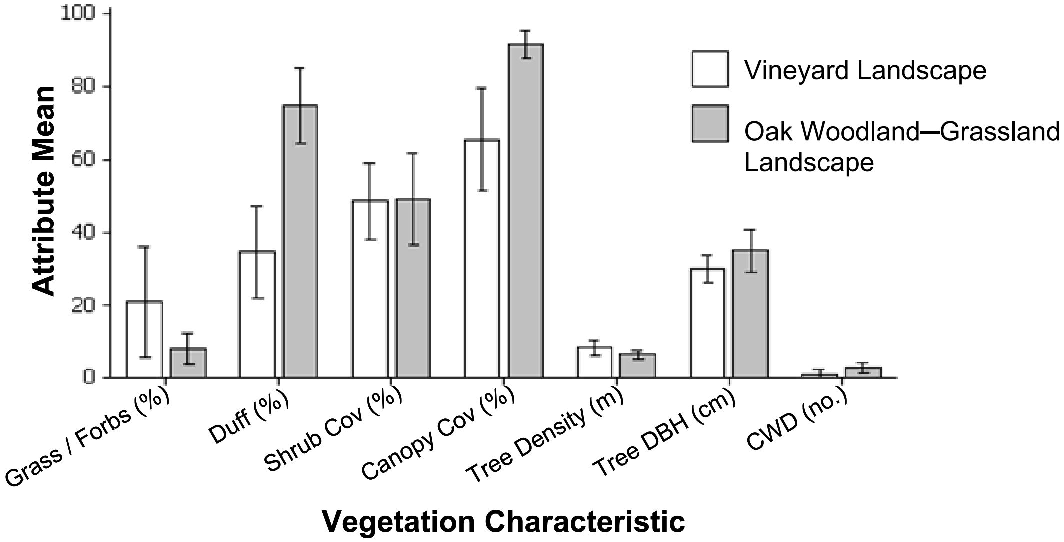


Figure 2—CI (95 percent) comparing selected vegetation attributes in Vineyard and Oak Woodland-Grassland Landscapes. Percentages of coverage for duff and tree canopy were greater in Oak Woodland-Grassland Landscape. All other vegetative characteristics means were not significantly different based on our sampling.

Birds

Species and Individuals

We recorded a total of 73 species of birds in the vineyard and oak woodland-grassland landscapes. We recorded a mean of 18.8 and 19.0 species, and 80 and 76 individuals, per 4 visits in the vineyard vs. oak woodland-grassland landscapes, respectively. Based on the 95% CI, the number of species and individuals between the two areas was similar.

Among the 10 bird species on vineyard landscape and oak woodland-grassland landscape that comprised the most individuals counted (*table 2*), nine were common to both treatments (bushtit, spotted towhee, oak titmouse, dark-eyed junco, western scrub-jay, California towhee, Bewick's wren, lesser goldfinch, and blue-gray gnatcatcher), and comprised 54% and 58%, respectively, of the total numbers of birds counted. During 120 point count visits in each of the two landscapes (30 stations x 4 visits/station), we detected 35 species more frequently on vineyard landscape (*table 2*). The difference in detection percentage was greatest for western scrub-jays (detected 82 of 120 visits in vineyard vs. 52 of 120 visits in woodland-grassland landscape = 37% difference).

Table 2—*Species most abundant by landscape type (species included were those that were detected 5 or more times). We calculated total count as the number of individuals identified over all 120 visits to point count stations. Mean and standard deviation (SE) are based on the four visits to 15 stations at each of the 2 replications of each landscape type. We counted 2,394 individuals in the Vineyard Landscape and 2,276 individuals in the Oak Woodland-Grassland Landscape.*

Vineyard Landscape				Oak Woodland-Grassland Landscape			
Species	**Count**	**Mean**	**SE**	**Species**	**Count**	**Mean**	**SE.**
Bushtit *(Psaltriparus minimus)*	237	30	17.99	Oak Titmouse	272	34	9.75
Spotted Towhee *(Pipilo maculatus)*	219	27	8.58	Bushtit	231	29	16.86
Oak Titmouse *(Baeolophus inornatus)*	217	27	22.52	Blue-gray Gnatcatcher	189	24	10.81
Dark-eyed Junco *(Junco hyemalis)*	168	21	13.62	Dark-eyed Junco	167	21	5.96
Western Scrub Jay *(Aphelocoma californica)*	163	20	7.78	Spotted Towhee	159	20	7.40
California Towhee *(Pipilo crissalis)*	137	17	4.32	Hutton's Vireo	140	18	6.39
Bewick's Wren *(Thryomanes bewickii)*	128	16	9.06	Bewick's Wren	128	16	4.17
Blue-gray Gnatcatcher *(Polioptila caerulea)*	121	15	16.45	Lesser Goldfinch	124	16	8.05
Lesser Goldfinch *(Carduelis psaltria)*	106	13	11.85	California Towhee	85	11	2.72
California Quail *(Callipepla californica)*	89	11	5.62	Western Scrub Jay	85	11	2.39
Hutton's Vireo *(Vireo huttoni)*	82	10	6.30	Pacific Slope Flycatcher	82	10	7.80
House Finch *(Carpodacus mexicanus)*	74	9	9.04	Orange-crowned Warbler	66	8	5.78
House Wren *(Troglodytes aedon)*	73	9	8.10	Anna's Hummingbird	48	6	4.38
Nuttall's Woodpecker *(Picoides nuttallii)*	61	8	4.41	Wilson's Warbler	44	6	4.17
Cliff Swallow *(Petrochelidon pyrrhonota)**	58	7	5.52	House Wren	40	5	2.83
Orange-crowned Warbler *(Vermivora celata)*	40	5	2.33	Warbling Vireo *(Vireo gilvus)*	40	5	5.42
Anna's Hummingbird *(Calypte anna)*	37	5	2.72	Nuttall's Woodpecker	37	5	2.67
Wrentit *(Chamaea fasciata)*	35	4	3.34	House Finch	35	4	5.40
Ash-throated Flycatcher *(Myiarchus cinerascens)*	30	4	5.70	Wrentit	27	3	1.77
Wilson's Warbler *(Wilsonia pusilla)*	30	4	3.45	Purple Finch *(Carpodacus purpureus)**	24	3	3.25
Turkey Vulture *(Cathartes aura)*	27	3	8.75	Ash-throated Flycatcher	23	3	1.25
White-crowned Sparrow *(Zonotrichia leucophrys)*	24	3	6.23	American Crow	19	2	3.96
California Thrasher *(Toxostoma redivivum)*	21	3	1.51	Violet-green Swallow *(Tachycineta thalassina)**	17	2	2.95

Vineyard Landscape				Oak Woodland-Grassland Landscape			
Species	**Count**	**Mean**	**SE**	**Species**	**Count**	**Mean**	**SE.**
Song Sparrow *(Melospiza melodia)*	19	2	1.06	California Quail	12	2	1.77
Bullock's Oriole *(Icterus bullockii)*	17	2	1.46	Northern Flicker	12	2	1.07
Mourning Dove *(Zenaida macroura)*	15	2	3.00	Brown-headed Cowbird *(Molothrus ater)**	11	1	1.85
American Crow *(Corvus brachyrhynchos)*	14	2	2.19	Lark Sparrow	10	1	1.39
Brewer's Blackbird *(Euphagus cyanocephalus)*	14	2	3.15	Black-chinned Hummingbird	9	1	1.13
Northern Flicker *(Colaptes auratus)*	11	1	1.19	Lazuli Bunting	9	1	1.64
Pacific slope Flycatcher *(Empidonax difficilis)*	11	1	1.41	Townsend's Warbler *(Dendroica townsendi)*	9	1	0.99
Barn Owl *(Tyto alba)*	10	1	1.28	Western Tanager	9	1	1.46
Lawrence's Goldfinch *(Carduelis lawrencei)**	10	1	1.49	American Robin *(Turdus migratorius)*	8	1	1.69
Red-tailed Hawk *(Buteo jamaicensis)*	10	1	1.04	Black-headed Grosbeak	8	1	1.41
American Kestrel *(Falco sparverius)**	7	1	1.73	Western Wood-Pewee *(Contopus sordidulus)*	8	1	1.85
European Starling *(Sturnus vulgaris)**	7	1	1.46	Bullock's Oriole	7	1	1.25
Lark Sparrow *(Chondestes grammacus)*	7	1	1.46	Steller's Jay *(Cyanocitta stelleri)**	7	1	1.13
Black-headed Grosbeak *(Pheucticus melanocephalus)*	6	1	1.16	White-breasted Nuthatch *(Sitta carolinensis)*	7	1	1.25
Lazuli Bunting *(Passerina amoena)*	6	1	1.39	Hermit Warbler *(Dendroica occidentalis)**	5	1	1.06
Yellow-rumped Warbler *(Dendroica coronata)*	6	1	1.49	Red-tailed Hawk	5	1	0.92
Black-chinned Hummingbird *(Archilochus alexandri)*	5	1	1.06	Yellow-rumped Warbler	5	1	1.41
Black Phoebe *(Sayornis nigricans)*	5	1	0.74				
Great Horned Owl *(Bubo virginianus)**	5	1	0.92				
Ruby-crowned Kinglet *(Regulus calendula)**	5	1	1.77				
Western Tanager *(Piranga ludoviciana)*	5	1	1.41				
Total Count	2,394			Total Count	2,276		

** Species unique to either vineyard or oak-woodland with a total individual count (from 120 visits) greater than four.

Unique Species

Of the 73 species we recorded five or more times, six were unique to vineyard landscape and five to oak woodland-grassland landscape (*table 2*). Of those unique species in vineyard landscape, cliff swallow, American kestrel, and European starling favor more open woodland habitat and are often associated with human development. In contrast on oak woodland-grassland landscape, of the five unique species, brown-headed cowbird, Steller's jay, and hermit warbler may be sensitive to habitat fragmentation.

Discussion

We detected similar bird assemblages in the wooded patches on our vineyard landscape and oak woodland-grassland study areas. This preliminary finding, if born out by further study, agrees with the conclusion that effects of agriculture on avifauna are complex and depend on particular species and ecological variables (Ormerod and Watkinson 2000). In contrast to temperate deciduous forests that have been fragmented the past century by agriculture, California oak woodland-grassland systems have been naturally patchy for millennia due to the influence on vegetation pattern of vegetation management during Native American occupation (Anderson 2006), soil fertility, seasonal rainfall, and plant intra- and inter-specific competition. Avifauna may have preadapted to an anthropogenically created patchy woodland-cropland system that has increased the past century. Therefore, some concepts of patch dynamics developed from studies conducted in eastern deciduous contiguous-canopy forest of the United States (Manson and others 1999; Demaynadier and Hunter 1998), may not so strongly influence bird assemblages in California oak woodland (e.g., patch size, edge vs. interior [Vreeland and Tietje 2004], isolation, source-sink populations). Importantly, however, the results of this study are preliminary, since they are based on only one season of point counts, only two treatments and two controls, and a small amount of data. Patch dynamics are not considered in this study. More study is needed to determine whether native fauna can or cannot persist in highly altered California oak woodland environments.

Patches of woodland surrounded by row crop development are increasingly becoming a common and ecologically important feature of California oak woodland landscapes. In addition to the implications of this study in California central-coastal oak woodland, a study by Reynolds and others (this volume) in two north coast counties found no evidence that the extent of vineyard development affected avifaunal nest success at the landscape scale. The authors conjectured that highly modified oak woodland landscape, if of sufficient size and properly managed, can support a diverse and productive avifauna. It is therefore important to work with landowners on management prescriptions that maintain and even restore and enhance landscape structures that maintain native bird assemblages. Ranches and farms often have available the materials and labor to provide some protection and restoration of "odd areas," including residual patches of habitat in which trees, shrubs, downed wood, and other habitat elements can be left in place without interference with agricultural production. Success is most likely when stakeholders are engaged collaboratively in the process (Ormerod and Watkinson 2000). A landowner can oftentimes take advantage of assistance programs provided by local government agencies. For example, Cooperative Extension, the Natural Resource Conservation

Service (NRCS), California Department of Forestry, and Land Conservancies are often eager for cooperators to engage in vegetation and wildlife enhancement, and demonstration projects. Such efforts will help maintain the rich avifauna native to California oak woodland.

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Continue

Nest Defense Behaviors of Native Cavity-Nesting Birds to European Starlings[1]

Rodney G. Olsen,[2] Kathryn L. Purcell,[3] and David Grubbs[4]

Abstract

We used behavioral experiments to evaluate competition for nest sites and the extent to which European Starlings (*Sturnus vulgaris*) are seen as a threat by native bird species at the San Joaquin Experimental Range, Madera County, CA. We quantified the level of aggressive behavior of four species of native cavity-nesting birds to starlings at active nests in trees and nest boxes. In 2000, we presented a life-like model of a starling at active nests of native cavity-nesting species, placed in front of the nest opening. In 2001, a House Sparrow (*Passer domesticus*) model was used as a control, with both species presented at nests. Models were mounted on a piece of wood and placed on top of the nest box. Responses were coded as sporadic scolding, continuous scolding, aggressive flight, and attack. Placement of the starling model in front of the cavity elicited a relatively more aggressive response than that elicited by a model placed on top of the nest box. Oak Titmouse (*Baeolophus inornatus*) responses consisted entirely of scolding except for one aggressive flight toward the model, but Western Bluebird (*Sialia mexicana*), Ash-throated Flycatcher (*Myiarchus cinerascens*), and Acorn Woodpecker (*Melanerpes formicivorus*) responses included physical attacks on the starling model. The starling model elicited a significantly stronger response from Oak Titmice and Western Bluebirds than the sparrow model. Although sample sizes were small, Ash-throated Flycatcher responses to the starling model included both aggressive flights and attacks, while neither behavior was seen in response to the sparrow model. Acorn Woodpecker response to the starling model at three nests tested was strong, consisting of attacks on the model by up to seven members of the group. Over the two years of the study, we observed nest usurpation and/or depredation by starlings at seven nests of five species. Our results show that Western Bluebirds, Oak Titmice, Ash-throated Flycatchers, and Acorn Woodpeckers recognize starlings as potential aggressors. We recommend the use of nest boxes to reduce the potential for nest-site competition between starlings and some native cavity-nesting species.

Keywords: Acorn Woodpecker, Ash-throated Flycatcher, cavity-nesting birds, European Starling, nest defense, nest-site competition, Oak Titmouse, Sturnus vulgaris, *Western Bluebird.*

Introduction

The European Starling (*Sturnus vulgaris)* was introduced to North America in 1890, and rapidly spread throughout most of North America (Kessel 1953). Their range in North America now extends from arctic Canada to the subtropics of Mexico (Feare 1984). Between 1968 and 1975, starling numbers increased an average of 16 percent per year (Robbins and Erskine 1975), rendering them one of the most abundant birds in North America. Starlings were first documented in California in 1942 (Jewett

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[2] Professor, Biology Department, Fresno City College, 1101 E. University Avenue, Fresno, CA 93741.

[3] Research Wildlife Biologist, Forestry Sciences Laboratory, Sierra Nevada Research Center, Pacific Southwest Research Station, Forest Service, USDA, 2081 E. Sierra Avenue, Fresno, CA 93710.

[4] Professor, retired, Department of Biology, California State University, Fresno, 5241 N. Maple, Fresno, CA 93740.

1942), and are now likely the most abundant Californian bird with numbers estimated in the tens of millions (Small 1994). By 1970, several nesting pairs were documented on the San Joaquin Experimental Range (hereafter SJER), located in the foothills of Madera County (Newman and Duncan 1973). During the last 25 years, starling numbers have increased dramatically at SJER (Purcell and others 2002). Starlings are now abundant nesters in both natural and excavated tree cavities throughout SJER and the foothill oak woodlands of California.

Starlings are aggressive nest competitors, known to evict native species from cavities (van Balen and others 1982, Ingold 1989, Kerpez and Smith 1990, Troetschler 1976) and even kill potential competitors for nest sites (Kessel 1957). Increases in starling abundance are expected to lead to decreased availability of nest cavities for native cavity-nesting species. Other than habitat loss, starlings may be the biggest threat to cavity-nesting birds in oak woodlands in California.

The objective of this study was to assess nest-site competition between European Starlings and native cavity-nesting bird species by examining whether starlings visiting a nest cavity were viewed as a threat by the current occupants of the cavity. We quantified the behavioral response of four species of native cavity-nesting birds to the presence of starlings at the nest site by performing behavioral trials at active nests. We also recorded incidental observations of aggression and nest usurpation by starlings.

Methods

Study Area

This research was conducted at the San Joaquin Experimental Range (hereafter SJER) in the western foothills of the Sierra Nevada, in Madera County, approximately 40 km north of Fresno, CA (*fig. 1*). SJER is 1,875 ha, with an elevation range between 215 and 520 m. The climate at SJER is Mediterranean, with cool, wet winters and hot, dry summers. Mean annual precipitation is 48.6 cm, 95 percent of which falls between October and April.

The vegetation is primarily blue oak foothill pine woodland (Mayer and Laudenslayer 1988) with blue oak (*Quercus douglasii*), interior live oak (*Q. wislizenii*), and foothill pine (*Pinus sabiniana*) as co-dominants. The sparse understory includes wedgeleaf ceanothus (*Ceanothus cuneatus*), chaparral whitethorn (*C. leucodermis*), and Mariposa manzanita (*Arctostaphylos viscida* ssp. *mariposa*). In drier areas, the vegetation is classified as blue oak woodland (Mayer and Laudenslayer 1988) and is dominated by blue oak with a grassland understory. SJER has been lightly to moderately grazed since the early 1900s, except for a 29 ha Research Natural Area that has not been grazed since 1934.

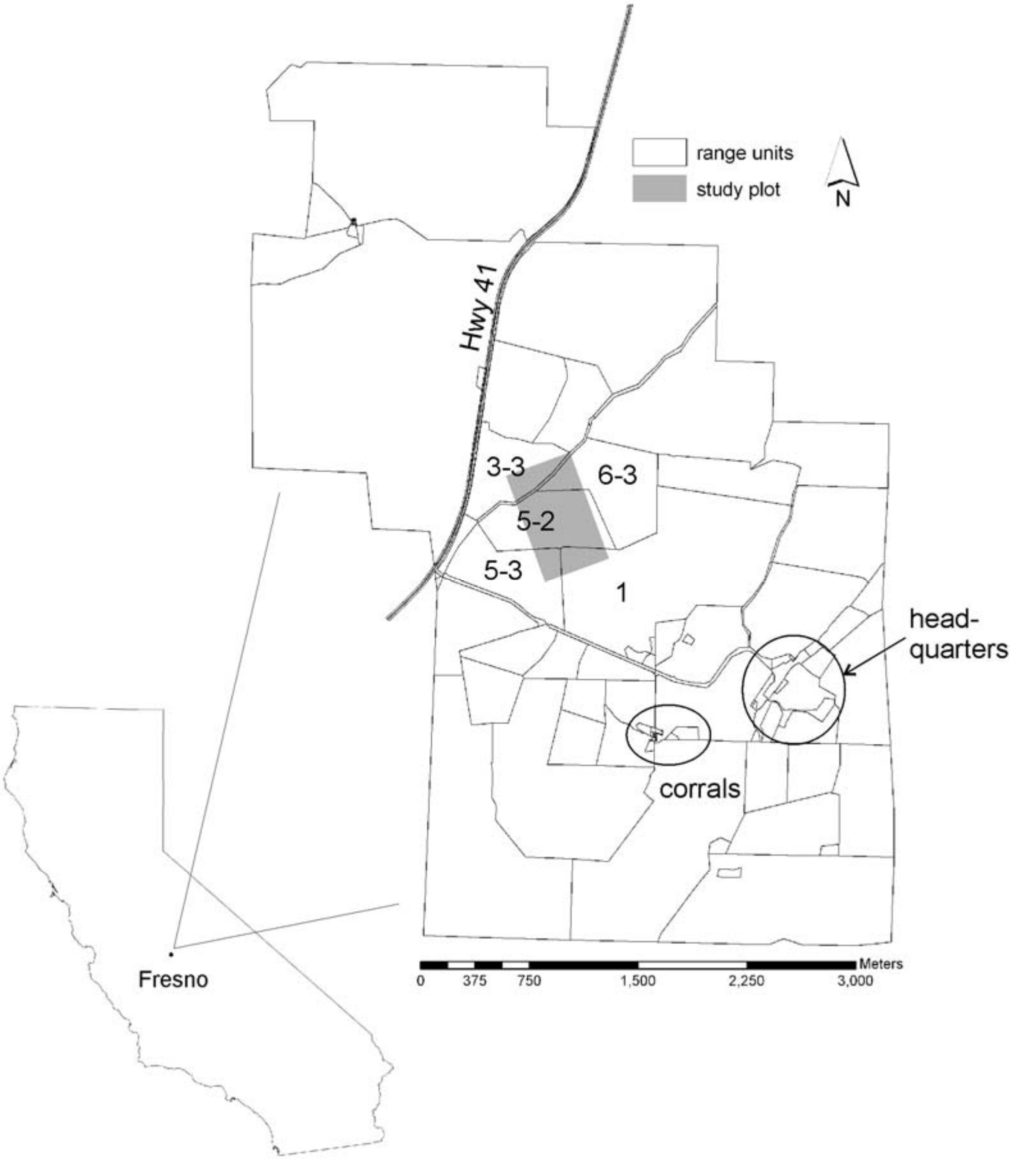

Figure 1—Map of San Joaquin Experimental Range showing range units and study plot.

Fieldwork

The cavity-nesting bird community at SJER includes two species of primary cavity nesters, Acorn Woodpeckers (*Melanerpes formicivorus*) and Nuttall's Woodpeckers (*Picoides nuttalli*), that excavate cavities used to a large degree by secondary cavity nesters. Secondary cavity nesters are particularly diverse in oak woodlands and at SJER, the most abundant of them include Ash-throated Flycatchers (*Myiarchus cinerascens*), Violet-green Swallows (*Tachycineta bicolor*), Oak Titmice (*Baeolophus inornatus*), White-breasted Nuthatches (*Sitta carolinensis*), Bewick's Wrens (Thryomanes bewickii), House Wrens (*Troglodytes aedon*), Western Bluebirds (*Sialia mexicana*), and European Starlings.

We located nests of cavity-nesting birds at SJER throughout the 2000 and 2001 breeding seasons. We primarily searched for nests on a 49 ha study plot located in grazed pastures (*fig. 1*), although we also searched for nests in other areas of SJER to increase sample sizes. Nests off the study plot were primarily located along roads accessing different portions of the study area in addition to areas near human habitation in the headquarters area.

In addition to nests in tree cavities, we monitored 59 pairs of nest boxes on the study plot, placed approximately 80 m apart. A pair of redwood nest boxes was randomly placed on major trunks of trees. Each box pair consisted of one box with an entrance diameter of 5.1 cm, and a box with either a 3.8 cm or 3.2 cm opening. Nest boxes with a 5.1 cm opening allowed access by both starlings and native cavity nesters, whereas boxes with smaller entrance diameters excluded starlings. Nest boxes were placed at a height of approximately 2 m.

Nests were examined regularly to determine activity and nesting stage. We used a fiberoptic scope to view the contents of nests in tree cavities in 2000 (Purcell 1997). To access cavities higher than 2 m, extension ladders and various tree climbing methods were used. In 2001, both the fiberoptic scope and a probing videocamera system (TreeTop I, Sandpiper Technologies, Inc.) were used.

We conducted behavioral trials at the nests of four species: Acorn Woodpecker, Ash-throated Flycatcher, Oak Titmouse, and Western Bluebird. We attempted to test responses of nesting birds during the incubation period to control for potential changes in nest defense behavior related to investment in the nest (Biermann and Robertson 1981), but this was not always possible. Of all nests tested, 80 percent were tested during the incubation period with the balance tested during the nestling period. No nests were used more than once to avoid problems of habituation or sensitization (Knight and Temple 1986).

Two types of behavioral trials were carried out to observe the responses of native cavity nesters to potential nest competitors. In 2000, we placed a life-like model of a starling near the entrance of active nests and recorded the behavioral responses of the nesting pair (*fig. 2*). The model was made using a euthanized starling trapped at SJER. The legs were reinforced with a light-gauge wire left projecting from the plantar region for attaching the model. The bird was arranged into a lifelike pose, wrapped in a paper towel, frozen at -80° C, and placed into a Vertis Vacu-station 1SL vacuum dehydrator for approximately 48 hours. The model was mounted on a blue oak branch.

Figure 2—For the 2000 behavioral trials, a European Starling model was positioned in front of the box.

Nests in both tree cavities and nest boxes were used for these trials. For nests in nest boxes, the model was presented by hooking the distal end of the branch under the hanging wire on the nest box. The model was positioned facing the box entrance no more than 0.2 m away (*fig. 2*). To present the model at cavity nests in trees, the model on the oak branch was attached to a telescoping pole and attached to the tree with a bungee cord. The model positioned approximately 0.5 m from the entrance of a nest cavity.

In 2001, we tested the responses of nesting birds to both starlings and a control species. We selected a female House Sparrow (*Passer domesticus*) as the control species for the following reasons. Female House Sparrows are characterized by drab coloration with no distinct markings except for a dull eye stripe. House Sparrows are a non-native species that are rare in oak woodlands outside of human habitation. Although there is evidence for nest-site competition between House Sparrows and Eastern Bluebirds (*Sialia sialia*) (Gowaty 1984), there is limited opportunity for interaction between sparrows and native cavity-nesters at SJER. At SJER they are uncommon and are found around buildings in the headquarters area only. They build nests in cavities, crevices, and shrubs near buildings and their nest sites may not be generally limiting due to the flexibility in nest site use (Stewart 1973). Thus, we assumed that House Sparrows would not be perceived as a threat to native cavity-nesting birds or that any response would provide a conservative test for comparison with starlings. A coin toss determined whether a nest was to be presented with the starling or the sparrow model.

The models were prepared using the same technique as in 2000, except they were mounted on a piece of wood the same dimensions as the roofs of the nest boxes. Models were presented at the nest by placing the mount on top of the box with the head of the model placed directly above the box entrance (*figs*. *3, 4*).

In both years, discreet observations were made of the activities of the nesting pair, prior to each test. If either member of the pair detected the observer during setup, the attempt was abandoned and no further trials were performed at that nest. When models were successfully deployed without detection, observations were made from an area of either suitable natural cover or a camouflage blind. Camouflage clothing was worn to reduce the chance of detection.

Figure 3—For the 2001 behavioral trials, a European Starling model was placed on top of the box.

Figure 4—A House Sparrow model placed on top of the box following the 2001 protocol.

The placement of the models for the 2001 breeding season was altered to decrease the chance of being detected by the nesting pair during setup. The 2000 season setup required several minutes at the nest to position the model correctly. On a few occasions we were detected by the nesting pair during the setup, obliging us to terminate the trial and exclude the nest from further trials. Placing the model on top of the nest box greatly decreased the time spent at the nest and the likelihood of detection by the pair. Consequently, only nests in nest boxes were tested in 2001.

In both years, observations were made for 3 minutes beginning when one member of the breeding pair acknowledged the model. Initial observations indicated a 3-minute trial was sufficient to observe the maximum response. Acknowledgment of the model was usually signaled by a change in the behavior of the bird. This could include a switch from foraging to posturing, a change from a foraging call to a scold, or physical aggression toward the model. We recorded two potential types of behavior during each trial—scolding and physical approach. Scolding was scored as sporadic or continuous. Sporadic scolding was defined as scolding for no more than a total of 1.5 minutes of the 3-minute observation. Continuous scolding lasted more than 1.5 minutes of the observation. Physical approach to the model was scored as aggressive flight or attack. Aggressive flight was defined as a deliberate flight toward the model within a 1 m radius of the model. Attack was defined as physical contact with the model. We also estimated the shortest distance between the nest occupant(s) and the model, and recorded whether either occupant entered the cavity during the trial.

Incidental observations of aggression associated with nest usurpation were recorded for all cavity-nesting species, both on and off of the study plot in the course of field activities. We attempted to identify the aggressor, subordinate, and victor species, as well as the nature and location of the interaction.

Statistical Analysis

We tallied the observations in each behavioral category by species, year, and model. For 2001, the numbers of each behavior observed in response to the starling and sparrow models were compared using a generalization of Fisher's exact test (Zar 1974) for Oak Titmouse and Western Bluebird. We set alpha equal to 0.10 due to small sample sizes and the low power of contingency table tests. For Oak Titmouse, we looked at only scolding behaviors (none, sporadic, and continuous) due to the small number of observations involving physical approach. For Western Bluebird, we examined both the scolding and physical approach variables. We compared responses to just the starling model in 2000 and 2001 to see if there was a differential effect of placing the model in front of the nest vs. on top of the nest box for Oak Titmouse (scolding only) and Western Bluebird (scolding and physical approach).

Results

Behavioral Trials

A total of 65 nests of the four species of native-cavity nesting birds tested in behavioral trials were located in tree cavities during the two years of the study. Three of the study species made an additional 117 nesting attempts in nest boxes. Acorn Woodpeckers did not use nest boxes, nor did European Starlings. Although starlings readily use nest boxes in other areas, they have not been observed to use them at SJER.

Oak Titmouse response to models consisted almost entirely of scolding, either sporadic or continuous. On only one occasion did a titmouse react with an aggressive flight toward the model, and no physical attacks on the model were observed. In 2000, behavioral trials were done at 17 Oak Titmouse nests using the starling model looking into the cavity. Titmouse scolding was sporadic at 24 percent of the nests and continuous at 76 percent of the nests tested (*table 1*). Based on only the scolding categories in 2001, the starling model elicited a stronger response than the sparrow model ($\chi^2 = 6.01$, df = 2, $P = 0.047$). Response to the starling model did not differ between years when the placement of the starling model was changed ($\chi^2 = 0.01$, df = 1, $P = 1.00$).

Table 1—*Oak Titmouse behavioral response to models of European Starlings (Starling) and House Sparrows (Sparrow) at nests, including the number of trials resulting in sporadic or continuous scolding, aggressive flight or attack, the number of trials where the occupants entered the nest, and the average approach distance to the model.*

Year		**2000**	**2001**	
Model		Starling (*N* = 17)	Starling (*N* = 12)	Sparrow (*N* = 10)
Scolding	**Sporadic**	4	3	4
	Continuous	13	9	3
Aggressive Flight		1	0	0
Attack		0	0	0
Entered cavity		4	4	4
Distance to model (cm)		75	88	151

Response of Western Bluebirds varied from sporadic scolding to attack (*table 2*). In 2000, behavioral trials were done at 13 bluebird nests. Scolding was scored as sporadic at 8 percent of the nests and was continuous at 31 percent, with no scolding noted at 17 percent of nests (*table 2*). Scolding may have been underestimated due to the distance from which the observations were made and the faint nature of Western Bluebird's call and scold notes. Aggressive flight was observed in 8 percent of the trials and physical attacks were observed in 77 percent. Physical attacks were fierce, sometimes involved both members of the pair, and included landing on the model, biting, and attempting to peck the eyes. Bluebirds went to the nest 15 percent of the time. In 2001, the only response to the sparrow model was sporadic scolding at two of the eight nests tested. Nest occupants presented with the starling model responded with aggressive flights in 43 percent of the trials and physically attacked the model in 14 percent of the trials (*table 2*). Response to the starling and sparrow models did not differ for the scolding variable ($\chi^2 = 3.61$, df = 2, $P = 0.184$), but bluebirds showed a significantly stronger physical approach response to the starling compared to the sparrow model ($\chi^2 = 5.33$, df = 2, $P = 0.077$). Bluebirds went to the nest 43 percent of the time when the starling model was used but always entered the nest when the sparrow model was used. Bluebirds responded more strongly to the starling model placed in front of the nest in 2000, compared to the model placed on top of the nest box 2001 in terms of both scolding ($\chi^2 = 5.93$, df = 2, $P = 0.090$) and physical approach ($\chi^2 = 7.43$, df = 2, $P = 0.023$).

Table 2*—Western Bluebird behavioral response to models of European Starlings (Starling) and House Sparrows (Sparrow) at nests, including the number of trials resulting in sporadic or continuous scolding, aggressive flight, and attack, the number of trials in which the occupant entered the nest, and the average approach distance to the model.*

Year		**2000**	**2001**	
Model		Starling ($N = 13$)	Starling ($N = 7$)	Sparrow ($N = 8$)
Scolding	**Sporadic**	1	4	2
	Continuous	4	1	0
Aggressive Flight		1	3	0
Attack		10	1	0
Entered cavity		2	3	8
Distance to model (cm)		55	106	10

Sample sizes for Ash-throated Flycatcher trials were low due to low nest numbers for this species coupled with the fact that they are sit and wait predators that can remain observant of the nest while foraging, increasing the incidence of detection during the set up. Both aggressive flights and physical attacks were observed in response to the starling model, but response to the sparrow model was limited to sporadic scolding (*table 3*).

Table 3*—Ash-throated Flycatcher behavioral response to models of European Starlings (Starling) and House Sparrows (Sparrow) at nests, including the number of trials resulting in sporadic or continuous scolding, aggressive flight, and attack, the number of trials in which the occupant entered the nest, and the average approach distance of the occupant to the nest.*

Year		**2000**	**2001**	
Model		Starling (*N* = 1)	Starling (*N* = 2)	Sparrow (*N* = 3)
Scolding	**Sporadic**	0	1	2
	Continuous	1	1	0
Aggressive Flight		0	1	0
Attack		1	1	0
Entered cavity		0	2	1
Distance to model (cm)		10	10	07

Acorn Woodpecker response was strong to the three trials performed on Acorn Woodpecker nests in 2000. In all three cases, one individual initiated the attack by making an alarm call and then flew in and attacked the model. This was followed by subsequent attacks on the model by other members of the group. Scolding and attacks were continuous throughout the observations. In two of the trials, there were at least seven woodpeckers involved in attacks on the model.

Nest Usurpation and Other Observations

In 2000, four nest usurpations of active nests by starlings were observed. An Oak Titmouse nest was usurped during the nest-building stage and occupied by a starling pair. The displaced titmouse re-nested in the same tree in another cavity with a smaller entrance. Both nests successfully fledged young. Two Western Bluebird nests were usurped, both during the building stage. In one case, bluebirds were observed bringing nest material into a cavity which starlings later occupied. At another cavity in a telephone pole, we observed fierce interactions between starlings and bluebirds over the cavity, including a male and female bluebird attacking and fighting to the ground a starling as it approached the nest. In subsequent days, we observed a starling intercepting the female bluebird and making physical contact as she made trips. The female bluebird was later found dead at the base of the pole. The starlings nested in the contested cavity. An active Ash-throated Flycatcher nest was usurped during the laying or incubation stage. When the cavity was checked, the clutch of three eggs noted on the previous visit was gone. A pair of flycatchers was observed at the nest but left the area after a pair of starlings entered the nest cavity. The starlings subsequently nested in the usurped cavity. It should be noted that three of the four usurpations observed in 2000 took place in nests located in the vicinity of human habitation and associated livestock corrals, where starling densities appear to be highest.

In 2001, three nest usurpations by starlings were recorded. We observed a White-breasted Nuthatch entering a cavity used by nuthatches the previous year and removing old material. Starlings occupied the cavity shortly after this observation. The same Oak Titmouse nest usurped in 2000 was also usurped by starlings in 2001. In this case, the titmouse did not re-nest in the same tree. We observed a starling inside an Acorn Woodpecker nest cavity that had contained four eggs on the previous visit. The woodpecker was calling aggressively. When the starling flew from the cavity, the woodpecker made an aggressive flight toward it. When checked, the nest was empty and eggshell fragments were found below the nest. As the starling did not nest in the usurped cavity, this appears to be a depredation event. Finally, at a Western Bluebird nest with three eggs, a starling was seen at the nest entrance after the nest was depredated. We lack evidence in this case to call it usurpation and there was no direct evidence that a starling was responsible for depredating the nest.

Other field observations of interactions between starlings and native species included Acorn Woodpeckers chasing starlings (one case) and starlings displacing Acorn Woodpeckers (three cases).

Discussion

One of the strongest arguments for competition is when aggression occurs over a limiting resource (Wiens 1989). Results of behavioral experiments and field observations in this study provide convincing evidence for competition between European Starlings and native cavity-nesting species at SJER. Data from behavioral experiments clearly show that Acorn Woodpeckers, Ash-throated Flycatchers, Western Bluebirds, and Oak Titmice recognized starlings as potential aggressors. Acorn Woodpeckers and Western Bluebirds reacted most strongly to starling models. Field observations of usurpations and direct aggression are indicative of interference competition between starlings and these four species and White-breasted Nuthatches.

An alternate interpretation of the nest defense behaviors observed here is that the behaviors observed were intended to repel predators rather than nest-site competitors. While we believe that the data from this study and others that have shown nest defense responses to starlings are most readily interpreted as resulting from competition for nest sites (e.g., Dobkin and others 1995, Ingold 1989, 1994, Kerpez and Smith 1990, Troetschler 1976, Weitzel 1988, Wiebe 2003), we are intrigued by the idea that European Starlings are nest predators as well. We recorded indirect evidence of mortality of an adult female Western Bluebird at a usurped nest. Direct mortality of adult birds of other species as well as conspecifics by starlings has been previously documented (Kessel 1957). In addition, we noted depredation of eggs by starlings on two occasions; in one case the starlings did not subsequently occupy the nest cavity. If starlings are nest predators, starlings may be further impacting native species by directly reducing their reproductive success. This question deserves further study.

Secondary cavity-nesting species are diverse and abundant at SJER. They are largely dependent on primary cavity nesters for nest sites and are potentially highly vulnerable to lowered availability of nest cavities, which are generally assumed to be limiting (Brush 1983, Cline and others 1980, Stauffer and Best 1982). An additional potentially aggravating factor related to nest-site limitation is the poor nest sanitation habits of starlings, which may render nests unusable to later nesting species (Feare 1984). Nevertheless, Acorn Woodpeckers also perceived starlings as a threat. We observed a strong reaction to starlings at nest sites and usurpation of Acorn Woodpecker nests by starlings, suggesting they are negatively impacted by starlings at SJER.

Western bluebirds overwhelmingly used nest boxes where they were available and may have shifted to nest boxes to reduce competition for nest cavities in trees. It is interesting to note that three of the five bluebird nests found in trees and poles were usurped by starlings during the two years of this study, and all bluebird nests not in nest boxes failed.

Starlings were most abundant around human habitation and high-density livestock areas at SJER, and the majority of random aggressive interactions between starlings and native cavity nesters took place in these areas. The high numbers of starlings in these areas may have increased the probability of interactions between starlings and native species, and the high incidence of aggression may be reflective of high starling densities rather than simply a lack of nest sites. On the other hand, high starling numbers and the relatively high starling nest densities in these areas likely constrain available nest sites for native species leading to competitive interactions over nest sites. Few direct incidences of direct aggression, aside from those elicited during behavioral trials, were observed on the study plot where starling densities were lower, even though much more time was spent on the study plot relative to time spent in other areas. In addition, the presence of nest boxes on the study plot may have reduced nest-site competition relative to areas without boxes.

Because energetic costs and physical risks related to aggression may be high, opponents should try to minimize risk through the suppression, reduction, or redirection of an attack (Moynihan 1998). For bluebirds, placement of the starling model in front of the nest box opening facing into the cavity elicited a more aggressive response than that elicited when the model was placed on top of the box. With the starling model on top of the box, bluebirds would often perch in a nearby tree and watch the model from above rather than attacking it as was the case when the model was in front of the cavity. In these cases, the bluebird may have been evaluating the necessity of aggression based on the location of the model. With the model on top of the box, the threat may not appear as immediate as the potential competitor may not have discovered the nest, reducing the possibility of depredation (Burhans 2000). Bluebirds detecting the model in front of the cavity appeared to perceive an immediate threat and acted more aggressively. In most cases, bluebirds reacted by physically attacking the model. These attacks were surprisingly intense and violent.

We expect more aggressive defense of nests by larger species. Although starlings are only slightly larger than Acorn Woodpeckers, they are roughly three times larger, in terms of mass, than Western Bluebirds and Ash-throated Flycatchers, and nearly five times heavier than Oak Titmice. The response levels noted in this study roughly correlate with body size. We noted the most violent response to starlings at nests by Acorn Woodpeckers and Western Bluebirds. Responses of the smaller Oak Titmice were limited to scolding.

The invasion of non-native species, coupled with habitat loss, may have significant harmful effects on the diversity and abundance of native species. We recommend further study of methods for reducing the impacts of European Starlings on native cavity-nesting birds. Previous work done at SJER indicated that starlings avoided ungrazed pastures and areas with deep litter (Purcell and others 2002). Research on the effects of litter depth and grass height could yield recommendations on grazing intensity and mowing practices that could help reduce starling numbers and their impacts on native bird species of California's oak woodlands. In areas where cavities are limiting, we recommend the use of nest boxes to reduce competition for nest sites. Nest boxes should have entrance diameters small enough to exclude starlings and should be monitored regularly to ensure that the openings have not been enlarged by woodpeckers, allowing access to starlings.

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Continue

Oak Ecology

Continue

Species Characteristics and Stand Structure of *Quercus garryana* and *Q. pyrenaica* Woodlands in the Mediterranean Regions of California and Spain[1]

Michael G. Barbour,[2] Stephen Barnhart,[3] Emin Ugurlu,[4] and Daniel Sanchez–Mata[5]

Abstract

Quercus garryana in western North America has a similar lack of recent regeneration as does *Q. pyrenaica* in Spain. Both species are deciduous white oaks whose ranges extend south to Mediterranean-type climates from more northerly temperate regions. Although the degree of genetic similarity and phylogenetic relatedness between the species is unknown, their degree of ecological convergence is remarkable in terms of geographical and elevational range, and in population characters such as density, canopy cover, basal area, frequency, and physiognomy. In Spain, both young stands (oldest individuals up to 90 years of age) and old-growth stands (individuals up to 368 years of age) were sampled. In California, two young stands and four intermediate-age stands (oldest individuals about 200 years of age) were sampled. The six California stands consistently had zero regeneration for the past 25 to 50 years and lower regeneration than expected for the past 50 to 100 years. Seven young *Q. pyrenaica* stands consistently showed regeneration below expectation during the past 30 years, and four old-growth stands exhibited lower regeneration than expected for the last 75 years. There was little evidence of high episodic past regeneration in any of the stands that would suggest the current period of low regeneration is a recurring pattern.

Keywords: Age structure, age-dbh relationship, California, Coast, convergence, forest ecology, Garry oak, melojo, montane vegetation, regeneration, physiognomy, succession.

Introduction

Poor regeneration among four species of white oaks in California has been described by a number of range ecologists since the 1960s (e.g., White 1966, Griffin 1971). More recent summaries by Allen-Diaz and Holzman (1991), Allen-Diaz and others (2007), Bartolome and others (1987), Bolsinger (1988), Muick and Bartolome (1987), Pillsbury and others (1997), and Waddell and Barrett (2005) concluded that poor regeneration (specifically the transition from seedling to sapling stages) has characterized the majority of *Quercus douglasii, Q. engelmannii, Q. garryana*, and *Q. lobata* stands for at least the past five decades.

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[2] Professor, Plant Sciences Department, University of California, Davis, CA 95616. e-mail: mgbarbour@ucdavis.edu.

[3] Professor, Biological Sciences Department, Santa Rosa Junior College, Santa Rosa, California 95401. e-mail: sbarnhart@santarosa.edu.

[4] Dr., Biological Sciences Department, Celal Bayar University, Manisa, 45100, Turkey. e-mail: emin.ugurlu@bayar.edu.tr.

[5] Professor, Biologia Vegetal II, Universidad Complutense, Madrid E-2804, Spain. e-mail: dsmata@farm.ucm.es.

Among the hypotheses that have been offered as an explanation for poor regeneration among these oaks are: competition between oak seedlings and exotic annual forbs and grasses; browsing of seedlings by deer and burrowing rodents; browsing of seedlings by domesticated livestock; absence of surface fires; compaction of soil by livestock, preventing seedling establishment; absence of sufficient shade for seedling survival; and invasion by other trees (*Pseudotsuga menziesii* in the case of *Q. garryana* woodlands; see Barnhart and others (1987, 1991). At this time, some supporting evidence exists for each hypothesis, but no overwhelming evidence for any one hypothesis.

Our objective in this paper was two-fold: to quantify the degree to which regeneration in stands of *Q. garryana* Dougl. ex Hook. (Garry oak or Oregon white oak) departs from values expected in a self-sustaining stand; and to see if a similar departure characterizes an ecologically similar taxon — *Q. pyrenaica* Willd. (melojo), which grows in Spain in a similar Mediterranean-type climate.

Garry oak is a white oak (i.e., it is in the subgenus and section *Quercus*). It is winter-deciduous, but tardily so (marcescent). Its distribution is mainly within the coast ranges, extending from San Francisco Bay north to Vancouver Island, covering 15 degrees of latitude (Burns and Honkala 1990). Within this span, the species occurs from sea level to 1,200 m elevation, but most commonly > 450 m. Mean annual temperature ranges from 8 to 18° C, and individuals are capable of tolerating hard frosts to -34° C. Although annual precipitation ranges from 17 to 263 cm, this species is considered to be drought-tolerant. *Q. garryana* is rated as intermediate in shade tolerance, although it is capable of reproducing in its own shade. Trees grow on Alfisols, Inceptisols, Mollisols, and Ultisols, all of moderate to strong acidity (pH 4.8-5.9). The species’ range covers approximately 600,000 ha, one-third of which lies within the state of California (Bolsinger 1988).

The elevation, climate, and associated species place Garry oak as an element of the mixed evergreen forest, defined by Sawyer and others (1988) and Barbour and Minnich (2000) as an ecotonal forest sandwiched between broadleaf-dominated foothill woodland below and conifer-dominated montane vegetation above. Other broadleaf tree species that characterize this forest include *Acer macrophyllum, Quercus chrysolepis*, and *Umbellularia californica*; conifers most often include *Pseudotsuga menziesii*. Stands may have a nearly closed canopy, either consisting of *Q. garryana* alone or mixed with conifer and broad-leaved evergreens in two distinct height classes, with few shrubs and herbs beneath. Alternatively, stands may have scattered trees with open canopies and a rich herbaceous understory. Mature trees reach 37 m tall and >200 cm dbh, attaining ages >300 years old. Sawyer and Keeler-Wolf (1995) and Sawyer and others (2007) have formally defined and characterized a Garry oak alliance that includes the geographic and compositional variations described above, but they have not yet described all of the associations.

Quercus pyrenaica Willd. (melojo) is a marcescent white oak tree species widely distributed throughout the Iberian Peninsula. Its northern limit extends to western France and its southern limit to the Rif Mountains of Morocco (Costa and others 1998, Rivas-Martínez and Sáenz 1991). It is almost exclusively restricted to siliceous substrates at elevations of 400 to 1,800 m (2,000 m in the Rif Mountains), receiving 400 to 1,200+ mm annual precipitation in meso- and supra-Mediterranean thermotype territories (a temperate bioclimate with a sub-Mediterranean character in some northern areas; the same bioclimate applies to the range of *Q. garryana*)

(Gavilán 1994, Gavilán and Fernández-Gonzalez 1997, Gavilán and others 1998, Rivas-Martínez and others 2002).

Q. pyrenaica typically forms a monospecific closed-canopy forest with low cover by understory shrubs and herbs. Its physiognomy is similar to that of mixed evergreen forest in California. Below the zone of melojo forest is an open woodland of *Q. rotundifolia*; with increasing elevation, melojo first shares dominance with, then yields to *Pinus sylvestris,* which thoroughly dominates a montane conifer forest. Like Garry oak, melojo occupies an ecotonal position between low-elevation broadleaf woodland and upper-elevation montane conifer forest.

Methods

In California, we selected a total of six Garry oak stands to sample, all within a 100-km radius of the city of Santa Rosa: two each at Annadel State Park, Warm Springs, and Pepperwood Preserve. The state park is immediately southeast of Santa Rosa and encompasses nearly 2,000 ha. Warm Springs is north of Santa Rosa and west of Healdsburg. It is a large public-access watershed around the Lake Sonoma Reservoir, managed by the Army Corps of Engineers. Pepperwood Preserve is a privately held reserve of approximately 1,200 ha northeast of Santa Rosa that is owned by the Pepperwood Foundation for the purposes of research and education. All three areas are dominated by volcanic substrates. We chose homogeneous stands uniformly dominated by Garry oak and located in areas protected from grazing and logging for at least the past 50 years. The stands varied in area from 1 to 20 ha. Elevation, slope, and aspect were measured for each, using a topographic map, inclinometer, and compass (*table* 1).

Table 1—*Locational data for* Quercus garryana *stands sampled in this study. All are mid- to late-seral stands located in Sonoma County, centering on 38°30’ N latitude x 123° W longitude. Area (ha) is the stand’s estimated extent, elevation is in meters, aspect is in degrees, and slope is in degrees.*

Location name/stand	Area (ha)	Elev (m)	Aspect (°)	Slope (°)
Pepperwood/1	10	240	345 (NNW)	40
Pepperwood/2	110	240	350 (NNW)	40
Annadel State Park/1	15	215	360 (N)	23
Annadel State Park/2	1	140	280 (NW)	10
Warm Springs/1	1	190	350 (NNW)	20
Warm Springs/2	1	210	315 (NW)	37

Within each stand we randomly located three circular plots, each 100-square-meters in size (radius = 5.6 m). In each plot, we measured the diameter breast height (dbh) of all Garry oaks, including standing dead individuals. In addition, all Garry oak saplings (defined as being < 1 cm dbh and > 20 cm tall) were counted, as were all Garry oak seedlings (defined as being < 20 cm tall). Then the entire stand was walked and ocular estimates of cover were made for each species of tree and shrub, for all trees (as a class), for all perennial bunch grasses (as a class), and for all annual herbs (as a class). Several trees, judged to be of average overstory height, were measured for both height and dbh. One or more individuals judged to be of maximum height and dbh were also measured. We used dbh and ring count data accumulated by Anderson and Pasquinelli (1984), who cored 27 Garry oak trees of various dbh (8 to 72 cm) in four locations within Sonoma County. We constructed our own linear regression of age as a function of dbh, from which we could assign ages to all trees we measured for dbh. Their locations were Warm Springs, a property owned by the California Academy of Sciences (8 km east of Windsor), Annadel State Park, and Sonoma Valley (7 km south of Kenwood).

In Spain, we sampled seven young stands, one intermediate stand, and four old-growth stands. The young stands were located in the Guadarrama Mountains portion of the Central System Range, 100 km north of Madrid. These showed no cut stumps nor evidence of disturbance by domesticated livestock or off-road travel by motorized vehicles. Locational information for the Spanish stands appears in Table 2. Based on the absence of any trees >100 years old, we surmised that all these stands had regenerated following some nearly synchronous catastrophic disturbance, such as clear-cutting followed by stump removal.

Table 2—*Locational summary* for Q. pyrenaica *stands sampled in this study. Latitude and longitude are given in degrees N and W, respectively; elevation is in meters, slope in degrees, and aspect (face) also in degrees. Area (ha) is the stand's estimated extent, and category refers to seral stage***.**

Stand	Region	Lat x Long	Elev	Slope	Aspect	Area	Category
1	Guadarrama	41°06 x 3°38	1380	14	45 (NE)	10	early
2	Guadarrama	40°50 x 3°48'	1360	20	235 (WSW)	14	early
3	Guadarrama	40°35' x 4°10'	1100	20	20 (N)	4	early
4	Guadarrama	40°53' x 3°50'	1420	19	350 (N)	50	early
5	Guadarrama	40°58' x 3°48'	1360	25	75 (ESE)	50	early
6	Guadarrama	40°56' x 3°52'	1360	20	160 (SSE)	4	early
7	Guadarrama	41°03' x 3°38'	1380	16	60 (ENE)	30	early
8	San Vicente	39°30' x 4°30'	1180	6	40 (NNE)	55	early-mid
9	Ancares	42°50' x 6°50'	1270	32	200 (SSW)	3	late
10	Cantabrica	43°9' x 4°31'	1095	26	205 (SSW)	2	late
11	Vitoria	42°40' x 2°30'	750	7	160 (SSE)	>1000	late
12	Mendilerroa	42°56 x 2°24'	710	6	175 (S)	2	late

For each selected stand, the elevation, slope, and aspect were noted, using an inclinometer, altimeter, and compass. The area of the stand was estimated. A record of the vegetation was taken in an area of 1,000 m^2 subjectively judged to be representative of the stand. All taxa present were estimated for cover/abundance. A 100-m long transect tape was randomly anchored and then laid out straight through the stand. Along it, a tally of all trees >1 cm dbh was kept for a belt 4-m wide by 100-m long, the center of the belt being marked by the transect tape. Every tree encountered was measured for its dbh. Dead trees (snags) were noted as dead and measured for dbh. The 400-m^2 sample area was chosen because it was large enough to enclose the stand. The collective cover of tree canopies and tree gaps along the tape was then estimated. Several trees, judged to be of average canopy height, were measured for their height by using an inclinometer. Two to three saplings of breast height were cut down at their base and one 2-cm-thick section of the base and another at breast height were taken back to the laboratory for drying, sanding, and ring counting. Approximately six uninjured and unsupressed trees with a range of diameters were subjectively chosen and cored at breast height, and the cores taken back to the laboratory for drying, sanding, and ring counting.

Two regions of northern Spain were visited to find old-growth stands: Two locales were chosen in the Montes de León region; and two other locales were chosen in Pais Vasco region. These four stands are in the Eurosiberian biogeographical region, having an oceanic temperate macrobioclimate with a submediterranean character (Rivas-Martínez and others 2002). No old-growth stands could be located in the Mediterranean-climate part of Spain.

The density of trees was much lower than in young stands, and for that reason the belt transect was increased in size to 8 x 100 m.

Results and Discussion

Quercus garryana

Our regression of tree age as a function of dbh—based on Anderson and Pasquinelli's (1984) data—generated a very strong linear relationship (*fig*. 1), years of age = [(6.22) x (dbh in cm)] — 13.43 with an R^2 value of 0.91 and a P = 0.001 that the slope departed from zero. Based on our formula, the largest tree we encountered (72cm dbh) would have had a predicted age of 434 years, not counting the additional number of years it would have taken to reach breast height.

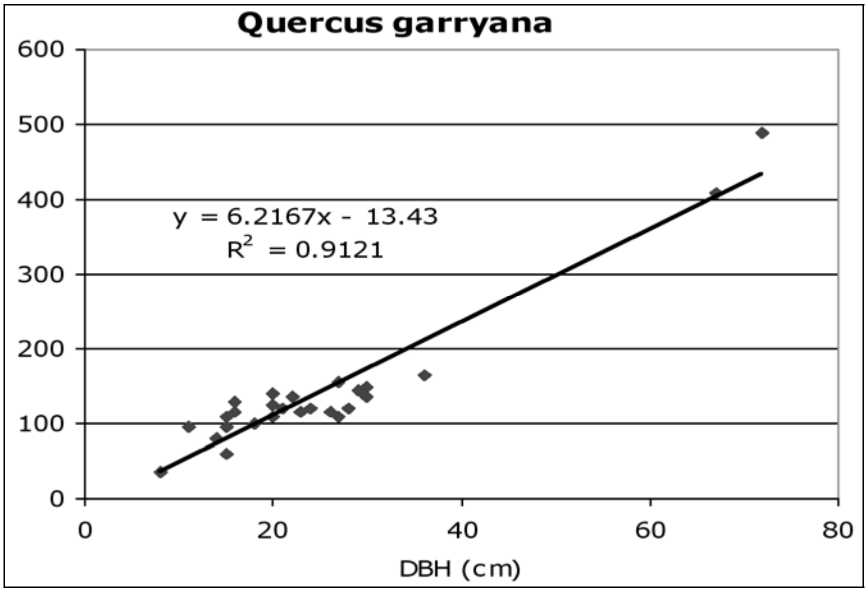

Figure 1—Regression of *Q. garryana* age against diameter breast height for 27 trees cored by Anderson and Pasquinelli (1984).

When we transformed our dbh data into years of age and expressed tree density per hectare, all three sites exhibited poor regeneration for as long as the past 50 to 100 years and zero regeneration for the past 25 to 50 years (*fig*. 2). Seedlings and saplings were completely absent from our plots, but an earlier study at Annadel State Park by Barnhart and others (1991) tabulated 178 seedlings per hectare. However, they were sampling woodland vegetation, in which herbs covered much of the ground. Three-fourths of the seedlings were found in understories dominated by perennial bunch grasses, mainly *Festuca californica*; the rest were found among invasive annuals. None of our six stands had an understory dominated by bunch grasses.

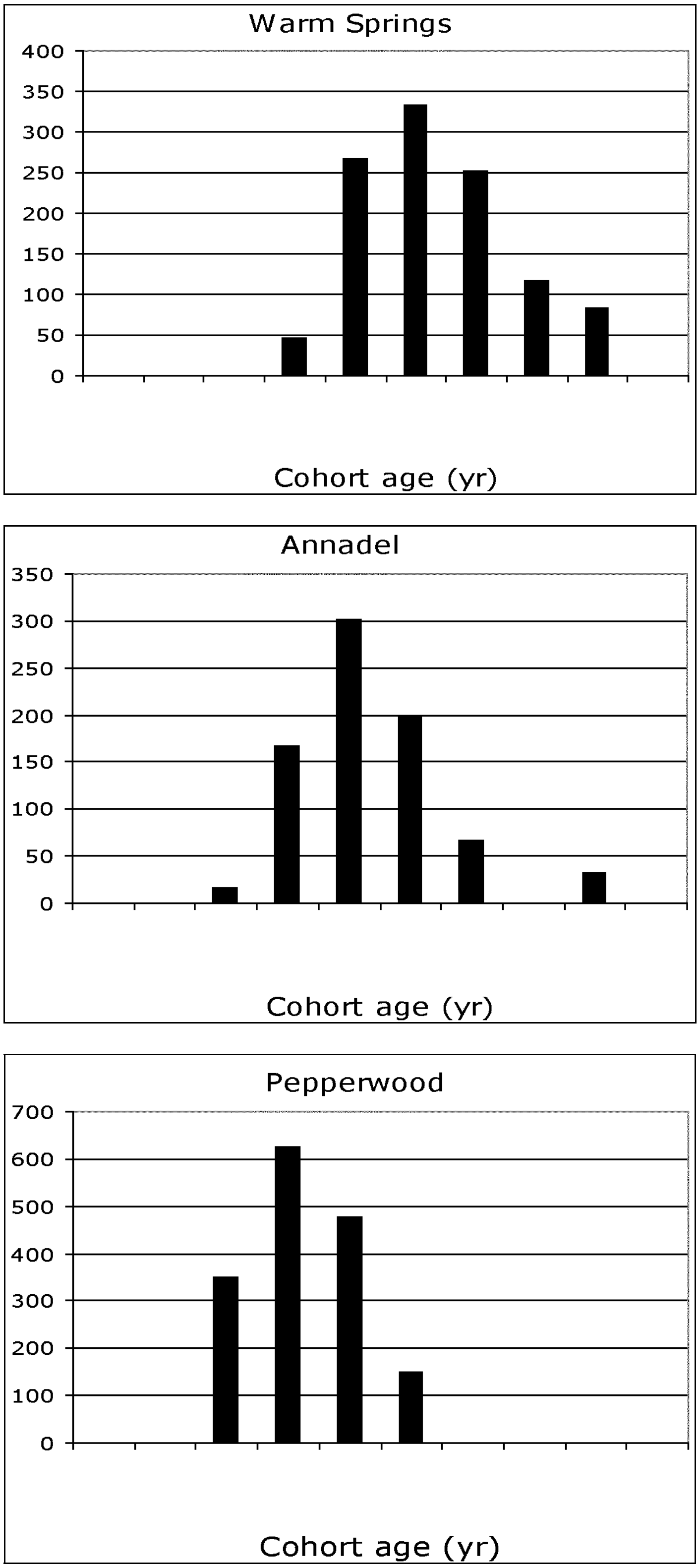

Figure 2—Stand age structure for *Quercus garryana* stands. (Top) Age structure for two Warm Springs stands combined. N = 70. (Middle) Age structure for two stands combined at Annadel State Park. N = 47. (Bottom) Age structure for the two younger Pepperwood stands combined. N = 64.

Tree density (*table* 3; defined as individuals > 1 cm dbh) was widely variable among the three sites: 600 to 1,100 per hectare at Annadel State Park and Warm Springs, and 1,500 to 1,600 at the younger Pepperwood stands. Standing dead trees were highest at Pepperwood, 12 percent of all (live + dead) trees, compared to 8 to 10 percent in the older stands at Annadel and Warm Springs. Only *Quercus garryana* was in the canopy at Pepperwood, whereas the other two forests included small numbers of *Quercus agrifolia, Pseudotsuga menziesii*, and *Unbellularia californica*. The Pepperwood forest had very little herbaceous cover, whereas the other two forests had high herb cover, typically > 70 percent.

Table 3—*Stand data for* Quercus garryana. *Mean tree canopy height is in meters; tree canopy cover is in percent; live tree density is per hectare; dead standing trees are shown in absolute numbers per hectare before the slash and as a percent of all trees, dead + live, after the slash. The last two columns summarize mean tree diameter breast height (cm) and basal area (square meters per hectare).*

Location and stand	Ht.	Canopy	Live	Dead / %	DBH mean	BA
Pepperwood, 1	11	53	1650	23 / 13	7	6.4
Pepperwood, 2	11	100	1550	0 / 0	6	4.7
Annadel, 1	9	73	635	0 / 0	22	22.9
Annadel, 2	11	88	802	133 / 19	19	22.6
Warm Springs, 1	9	75	1069	133 / 11	22	38.5
Warm Springs, 2	9	83	1136	65 / 5	26	61.3

Quercus pyrenaica

Vegetation in seven early-successional stands had high densities of small-diameter trees (*table* 4; 1600-11,500 per ha), with pronounced mortality, averaging 16 percent of all trees (dead plus live). Common associates in these stands include the shrubs *Genista florida* subspecies *florida, Crataegus monogyna*, and *Rubus ulmifolius,* and the perennial herbs *Pteridium aquilinum, Poa nemoralis, Holcus mollis, Arenaria montana, Clinopodium arundanum*, and *Luzula forsteri*.

Table 4—*Stand data for* Q. pyrenaica. *Stands 1-7 are young stands; stand 8 is intermediate, and stands 9-12 are old-growth. Height mean/max is in meters. Cover is in percent (for tree + shrub + herb canopies). Mean diameter breast height (dbh) is in centimeters. Density is number of live* Q. pyrenaica *trees >1 cm dbh per hectare/percent of all trees that were dead. Basal area is in square meters per hectare.*

Stand	Height	Cover	Mean dbh	Density/dead	Basal area
1	10 / 15	96 / 2 / 5	10	5720 / 21	4.5
2	11 / 14	97 / 1 / 1	9	11,200 / 2	7.1
3	7 / 11	75 / 1 / 2	12	4600 / 13	5.2
4	9 / 12	93 / 0 / 1	10	10,000 / 22	7.8
5	12 / 14	93 / 1 / 2	9	9250 / 18	5.8
6	13 / 17	93 / 1 / 2	11	6000 / 23	5.7
7	11 / 13	96 / 1 / 2	10	11,500 / 18	9.0
8	14 / 19	80 / 1 / 1	16	1600 / 12	24.5
9	16 / 20	64 / 20 / 3	27	513 / 0	29.2
10	17 / 20	100 / 1 / 1	37	500 / 0	53.4
11	20 / 23	95 / 2 / 2	26	475 / 3	25.0
12	15 / 17	69 / 13 / 1	21	563 / 0	19.4

Although we were unable to find successional young stands of *Q. garryana* in California, we found many young stands of *Q. pyrenaica* (finding mature stands was difficult) and decided to summarize their composition and structure separately. For the purposes of this study, we defined young stands as having a mean dbh <12 cm, mean tree height <14 m, density per hectare >1,500, and an absence of trees >100 years old. We defined old-growth stands as having a mean dbh >20 cm, mean tree height >14 m, a density per hectare <600, and the presence of many trees >200 years old. We propose that these young stands were initiated following some stand-replacing disturbance such as clear-cutting or fire.

Stand 8, in the Montes de Toledo, appeared to be a mid-seral forest, given the intermediate dbh, height, and density of trees. Unfortunately, the cores from trees at this site have been lost, so we have no age data for that stand.

The late-successional stands had densities only 1/3 to 1/2 of young stands (averaging about 500 trees per ha) and practically no mortality, possibly indicating that self-thinning had ended some time in the past. Stumps were absent, indicating that snags had not been harvested for the past several decades. Somewhat surprisingly, although the mean canopy height of old-growth trees was significantly ($P < 0.01$) taller than that of young stands, the difference was modest: 16.0 vs. 11.0 m. Most allocation of photosynthate over time, therefore, must be channeled to the root system and/or stem girth.

When all 45 cores from stands 1-7 had been counted and graphed against dbh, a linear regression line having the formula age in years = [(1.41) x (dbh in cm)] + 21.31 was the result. It has a slope significantly different from zero ($P < 0.001$) and an R^2 of 0.69. When the 1,152 dbh records taken from belt transects in stands 1-7 were converted to ring age classes (*fig*. 3), the age structure of the combined seven stands showed: (1) almost 2/3 of all trees were between 30 and 39 years of age, (2) almost zero regeneration characterized the most recent 30 years, and (3) the oldest tree encountered was just over 90 years old—possibly a remnant from a previous forest harvested half a century ago or one that had stood alone in a cultivated field that was abandoned.

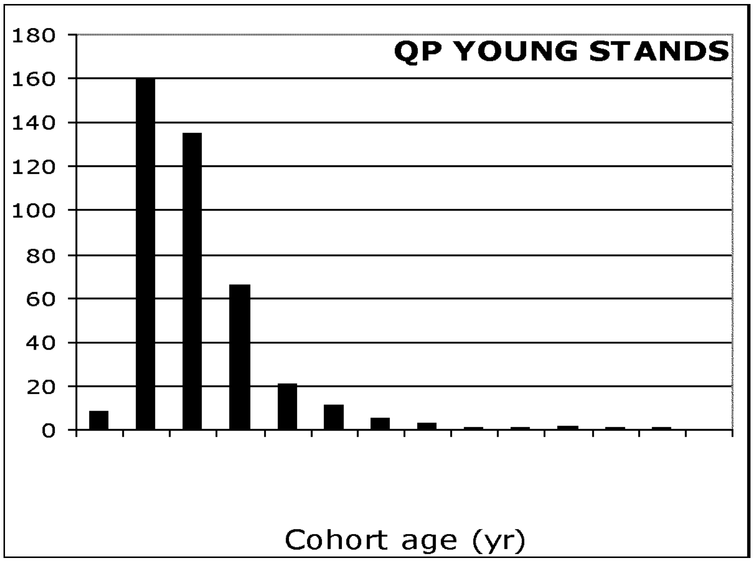

Figure 3–Age structure for seven young stands of *Quercus pyrenaica* combined. N = 1152.

Twenty trees in the four old-growth stands were cored. For those trees with a diameter too large for our increment corer to reach the center, the missing number of rings was estimated as follows. The rings along the length of the extracted core were counted and divided by the length of the core (excluding bark) to obtain an average number of rings per centimeter. The missing centimeters of core were estimated by subtracting the extracted core's length from the radius of the tree (again, excluding bark). The predicted number of missing rings was calculated by multiplying the missing core length times the average number of rings per centimeter, and the missing rings were then added to the counted rings to obtain an estimate of tree age.

The regression line for dbh against ring count fits the formula, age in years = (3.56) (dbh in cm) – 22.20, with an R^2 of 0.81. The slope of increasing age with girth (3.56) is steeper than that for young stands (1.41), which is in agreement with our conclusion earlier that the allocation of photosynthate in older melojo trees goes more towards increasing trunk girth than to increasing height.

When all 164 diameters, from all four stands, were converted to age, the combined age structure showed an absence of regeneration for the past 5 years and depressed regeneration 6 to 75 years ago, a peak of trees in the 76 to 100 year-old cohort, and a smoothly declining abundance of older trees, the oldest being (an estimated) 351 to 375 years old (*fig.* 4). Maximum dbh was 93 cm, three to five times the maximum for early-successional stands.

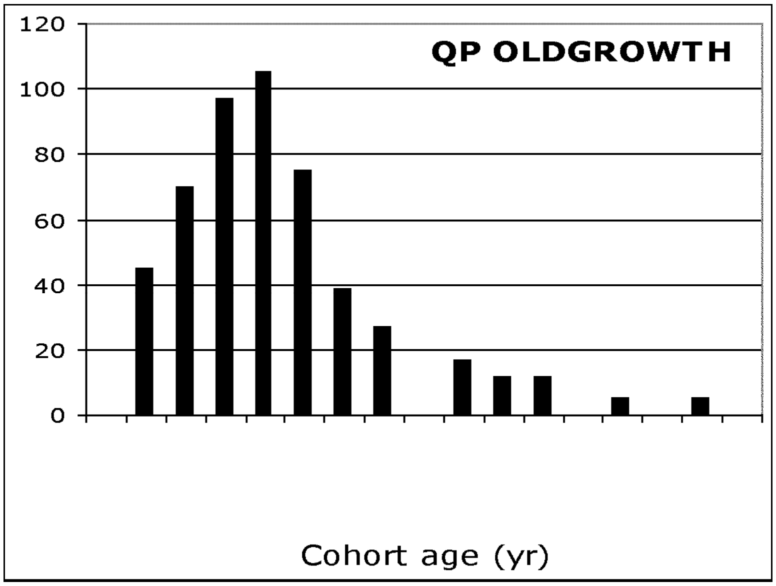

Figure 4—Age structure for four old-growth stands of *Quercus pyrenaica* combined. N = 165.

Thus, both young and mature stands of *Q. pyrenaica* show depressed regeneration for the past 75 years. Is this depression a result of human (mis)management, which can be corrected, or does it merely reflect a natural cycle where pulses of establishment are separated by long periods of regeneration failure? And if the latter, what causes the pulses: unusual weather, fluctuations of herbivore populations, masting behavior? If we suspect natural cycles on the order of one per century, then figure 3 does not provide much support, for it fails to show obvious second or third peaks for cohorts 200 or 300 years old. (Such peaks would be lower than the 100-year-old peak, because of more accumulated mortality, but there is actually an absence of individuals in those cohorts.)

The distributional and physiognomic similarities of young and old Garry oak and melojo oak stands are obvious and striking. *Q. pyrenaica* and *Q. garryana* appear to be convergent not only in habitat, tree morphology, phenology, community architecture, and their ecotonal nature, but also in their unexplained regeneration failure for the better part of the past century.

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Continue

Molecular Markers Show How Pollen and Seed Dispersal Affect Population Genetic Structure in Coast Live Oak (*Quercus agrifolia* Née)[1]

Richard S. Dodd,[2] Zara Afzal-Rafii,[2] and Wasima Mayer[2]

Abstract

Coast live oak (*Quercus agrifolia* Née) occurs in the coast range mountains from southern Mendocino County, California, to the Sierra San Pedro Martir, Baja California, Mexico. In Northern and Central California, coast live oak is suffering heavy mortality as a result of infection by *Phytophthora ramorum*. Earlier studies indicated biochemical differentiation of central coast populations from those of Northern and Southern California, an important hybrid zone in Northern California. A possible differential response to inoculation between populations from Northern and Southern California has also been reported. Here, we report results of a rangewide genetic diversity study of this species using chloroplast and nuclear microsatellite markers. The chloroplast genome is inherited maternally and its dispersal is limited because of the relatively large heavy seeds of oaks. We analyzed chloroplast microsatellites in more than 500 individuals from 41 populations and nuclear microsatellites in about 500 individuals from 28 populations of coast live oak from throughout its range. Based upon the chloroplast haplotype distributions, at least four biogeographic groups were detected. Nuclear microsatellite markers revealed reduced levels of genetic structure as a result of pollen dispersal. We discuss the roles of seed and pollen dispersal in the evolution of populations of coast live oak and how this information may help in developing strategies for studies of resistance to the sudden oak death disease.

Keywords: Biogeography, chloroplast DNA, genetic structure, pollen, Quercus*, seed.*

Introduction

Post-European settlement of California has brought substantial and rapid changes to the ecology of oak woodlands. Early Spanish settlement introduced large-scale ranching that reduced continuous stands to pockets of residual woodland, particularly in the inland valleys. Subsequent human population expansion has resulted in urban and suburban development and conversion of woodland for agriculture that have furthered the process of fragmentation of oak woodland. A theoretical consequence of fragmentation and decreased population sizes is reduced genetic diversity as populations become increasingly isolated and suffer from the stochastic consequences of genetic drift (Hedrick 2005). Genetic diversity has been linked to fitness traits (Frankham 2003, Charpentier and others 2005) and may enhance ecosystem recovery following environmental extremes (Reusch and others 2005). Therefore, the future management for healthy oak woodlands requires an understanding of the level and distribution of genetic variation, so that maximum

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[2] Department of Environmental Science Policy and Management, 137 Mulford Hall, University of California, Berkeley, CA 94720.

genetic variation can be conserved and appropriate genetic resources can be selected for restoration.

The traditional approach for forest tree species was to establish replicated provenance studies to detect genetic variations in adaptive traits (Morgenstern 1996). However, provenance studies are costly and require a long time to obtain results. Molecular markers, such as microsatellites, permit the estimation of neutral genetic variance and its partition as a result of the balance between gene flow and genetic drift. By comparing genetic structure of nuclear DNA with that of chloroplast DNA (*cp*DNA), the effects of gene flow by seed can be distinguished from that of pollen. Ennos (1994) estimated gene flow by pollen to be about 200 times more important than gene flow by seed in European oaks. Therefore, it is to be expected that a stronger pattern of genetic structure would be discerned for *cp*DNA than for nuclear DNA. Also, the two molecular systems may provide different information on population structure. The chloroplast genome is particularly useful for inferring the migration of lineages over evolutionary time because of its slower mutation rates and its smaller effective population size (Petit and others 1997). Whereas, the more rapidly evolving nuclear genome is ideal for studying rates and direction of gene flow (Beerli and Felsenstein 1999).

Coast live oak (*Quercus agrifolia* Née) occupies the coastal mountain ranges from the southern Ukiah Valley, Mendocino County in Northern California, to the Sierra San Pedro Martir in Baja California, Mexico. Urban development has heavily impacted populations in Southern California, and ranching has fragmented populations in the interior valleys. In the last 10 years, sudden oak death has brought heavy mortality in some areas of Northern California. coast live oak occupies areas that are likely to see substantial climatic change over the next century, with increasing humidity in the southwest and increasing aridity in the north (Hayhoe and others 2004). The habitat envelope that is defined by a Mediterranean climate under the influence of summer fog may become more limiting in the future.

Here, we present data on a study of *cp*DNA and nuclear DNA diversity throughout the range of coast live oak to detect possible geographic structure that would be useful in conservation of genetic resources.

Methods

Leaf samples were collected from 505 individuals from 38 populations for chloroplast DNA analysis and from 499 individuals from 28 populations for nuclear DNA analysis. Populations were selected to cover the geographic range of the species (*table 1*) and included the type variety *agrifolia* and var. *oxyadenia* from San Diego County and from Baja California, Mexico. Variety *oxyadenia* was identified by the dense tomentose undersurface of the leaf. The leaves were stored in plastic zipper-loc bags at -20°C.

Total genomic DNA was extracted from the leaf samples using a simplified CTAB (cetyltrimethyl ammonium bromide) method (Cullings 1992).

Chloroplast Microsatellites

Five pairs of primers developed for the amplification of chloroplast microsatellite loci (*μdt1*, *μdt3*, *μdt4*, *μcd4*, *μdt5*) in *Q. petraea* and *Q. robur* (Deguilloux and others 2003) were chosen to amplify chloroplast DNA in coast live oak. The PCR reaction solution (10µl) contained four dNTPs (0.2mM each), 2.5 mM of $MgCl_2$, 0.2µM of each primer, 10x reaction buffer, 25ng DNA and 1 unit of Amplitaq polymerase (Applied Biosystems, Foster City, CA). Amplifications were performed on a Techne Genius thermal cycler with the following profile; 5 min denaturing at 95°C, followed by 25 cycles of 1 min denaturing at 94°C, 1 min annealing at the primer T_m (see Table 1 in Deguilloux and others 2003) and 1 min extension at 72°C, with a final extension of 72°C for 8 min. The PCR product (0.75 µL) was mixed with a solution of 8 µL of formamide and 0.5 µL of 350 ROX size standard (Applied Biosystems, Foster City, CA) and electrophoresed on an ABI 3100 automated sequencer (Applied Biosystems, Foster City, CA). Results were analyzed with GENESCAN 3.7 and GENOTYPER 3.7 software (Applied Biosystems, Foster City, CA).

Nuclear Microsatellites

Six pairs of primers developed for the amplification of nuclear microsatellite loci (*quru-GA-0A01*, *quru-GA-0C11*, *quru-GA-0C19*, *quru-GA-1C08*, *quru-GA-1F02*, *quru-GA-2F05*) in *Quercus rubra* (Aldrich and others 2002) were used to amplify nuclear DNA in coast live oak. Amplifications were performed in a standard polymerase chain reaction (PCR) mixture containing a buffer of 2.5mM Tris-HCl (pH 8.0), 12.5 µM EDTA, 125 µM DTT. We added 2.5 mM $MgCl_2$, 2.5mM each of the amplification primers, 2.5µM of each dUTP, 250µg/mL BSA and 0.0375 units/µL of Taq DNA Polymerase (Invitrogen). To facilitate PCR multiplexing, we used a touchdown program to optimize for differences in annealing temperature. The PCR reaction began with one activation cycle at 95°C for 10 min and then used the following cycle parameters: a denaturation phase of one minute at 94°C, one minute at 60°C and 35 seconds at 70°C for two cycles. The second phase followed for 18 cycles: 45 seconds at 93°C, 45 seconds at 59°C (reducing the annealing temperature by 0.5°C each cycle) and 45 seconds at 70°C. Following this phase were 20 cycles of 30 seconds denaturing at 92°C, 30 seconds at 50°C and 1 min extension at 70°C. This was followed by a final extension phase of 5 min at 72°C.

We used fluorescently labeled primers to visualize amplified PCR products on an Applied Biosystems 3100 automated sequencer. A two uL aliquot of PCR product was suspended in 8uL of formamide and 0.5uL of ROX 350 size standard (Applied Biosystems) and denatured for 4 minutes at 93°C. Genotypes were scored by length in base pairs using GENESCAN 3.7 and GENOTYPER 3.7 software (Applied Biosystems, Foster City, CA) and recorded in a Microsoft Excel spreadsheet.

Data Analysis

Because the chloroplast genome is inherited clonally, we combined the five microsatellite loci into a single haplotype for each individual. Nuclear microsatellites were treated as independent loci with two alleles. We ran global tests of population differentiation and analysis of molecular variance using the Weir & Cockerham (1984) estimate of θ for small population size as implemented in FSTAT (Goudet 2001). For nuclear microsatellites, we evaluated allelic richness (A) and expected heterozygosity (H_e) as measures of population genetic diversity using Fstat vers. 2.9.3 (Goudet 2001). A is highly dependent on population size, therefore we used a rarefaction procedure recommended by El Mousadik & Petit (1996), as implemented in FSTAT. FSTAT estimates the number of alleles in a sample corrected to the smallest population sample-size, for all populations.

Table 1—*Sampling localities and sample size (N_c–chloroplast, N_n-nuclear) for coast live oak (*Quercus agrifolia*). Genetic diversity indices (A – allelic diversity and H_e – heterozygosity) for nuclear microsatellites shown.*

Population location	County	Latitude	Longitude	N_c	N_n	A	H_e
Hopland	Mendocino	38.9874	123.0826	18	31	0.820	4.06
Yorkville	Mendocino	38.8705	123.0826	6			
Cloverdale	Sonoma	38.8152	122.9385	11	9	0.785	3.92
Geysers Rd	Sonoma	38.8262	122.9153	9	9	0.817	4.01
Forestville	Sonoma	38.4723	122.9201	10	10	0.838	4.19
Monticello Rd	Napa	38.3557	122.2086	13			
Rockville Hills Park,	Solano	38.3070	122.1291	9			
Cordelia	Solano	38.2167	122.1145	10			
Novato	Marin	38.0496	122.5363	43	47	0.582	2.91
Nicasio	Marin	38.0662	122.7055	9	9	0.604	2.96
China Camp State Park	Marin	38.0057	122.4827	68	77	0.581	2.96
Lafayette	Contra Costa	37.9304	122.1664	12			
Sunol	Alameda	37.6070	121.8739	10			
Morgan State Park	Contra Costa	37.8264	121.8008		52	0.617	3.00
Huddart Park	San Mateo	37.4263	122.3114	7			
Saratoga Pass	San Mateo	37.3726	122.2580	10			
Hwy92/Hwy 280	San Mateo	37.5111	122.3496	9			
Soquel	Santa Cruz	37.1128	121.9098		7	0.703	3.55
UC Santa Cruz campus	Santa Cruz	36.9938	122.0627	5			
San Juan	San Benito	36.8054	121.5819	12	7	0.380	2.10
Pacheco State Park	Merced	37.0666	121.2009	22	10	0.562	2.74
Hwy 152	Merced	37.0346	121.2018		32	0.646	3.10
Monterey	Monterey	36.5699	121.9007	12			
Bottchers Gap	Monterey	36.3316	121.7961	11			
Palo Colorado Canyon	Monterey	36.3940	121.8785	9	8	0.646	3.02
Molera State Park	Monterey	36.2874	121.8467	10	34	0.662	3.19
San Miguel	Monterey	35.8352	120.6270	15	10	0.664	3.28
Parkfield	Monterey	35.9079	120.5518	9	9	0.694	3.50
York Mtn Rd	San Luis Obispo	35.5395	120.8029	17	16	0.643	3.16
Chorro Creek	San Luis Obispo	35.3492	120.7972	12	11	0.676	3.34
Ojai	Ventura	34.4293	119.1210	14	11	0.646	3.15
Lebec	Kern	34.8779	118.8975	4	9	0.618	2.93
San Gabriel	Los Angeles	34.2980	117.8412	6			
El Cariso	Riverside	33.6478	117.4170	12	12	0.606	3.06
Morettis Jnctn	San Diego	33.2055	116.7251	10	9	0.689	3.36
Santa Ysabel	San Diego	33.1479	116.6754	11	11	0.616	3.04
Julian	San Diego	33.0984	116.8042	13	13	0.679	3.43
Peutz Vlly	San Diego	32.8502	116.8042	12	11	0.749	3.81
La Mission	Baja Norte	31.9840	116.7243	10	10	0.604	3.00
St. Thomas	Baja Norte	31.5806	116.4179	11	11	0.629	2.95
San Pedro Martir	Baja Norte	30.9727	115.7695	14	14	0.602	2.87

By simultaneously combining spatial and genetic distance data, hypotheses concerning geographical pattern and genetic differentiation can be developed. We investigated geographical locations where genetic barriers among populations might occur using the software BARRIER vers. 2.2 (Manni and others 2004). This analytical method makes use of Monmomier's maximum difference algorithm (Monmonier 1973) to find edges associated with the highest rates of change in a distance (genetic distance) matrix. The algorithm is applied to a network of geographic distances among populations using Delaunay triangulation (Brassel & Reif 1979). Barriers are placed perpendicular to edges that correspond to the largest genetic distances and are continued across adjacent edges in order of maximum genetic distance until the barrier reaches the limit of the network space, or a previously determined barrier. We chose BARRIER over other programs, such as STRUCTURE (Pritchard and others 2000) and GENELAND (Guillot and others 2005), because the algorithm is not dependent on underlying genetic properties such as Hardy-Weinberg equilibrium within groups and linkage equilibrium among loci as are STRUCTURE and GENELAND. The chloroplast genome is clonally inherited and so, loci are fully linked. For the nuclear genome, we used Slatkin's linearized F_{st} (Slatkin 1995) genetic distances among populations for input into BARRIER. For the chloroplast genome, we treated the haplotype (5 linked loci) as a locus and each different haplotype as an allele. Analysis of molecular variance was used to generate a genetic distance matrix of Φ_{st} (an analog of F_{st}) that was input into BARRIER. Re-sampling random subsets of individuals within populations provided 100 bootstrap replicate distance matrices to obtain statistical confidence for the predicted barriers.

Results

Chloroplast DNA

A total of 31 haplotypes were detected. Analysis of molecular variance showed that 94 percent (95 percent confidence limits 90.9 to 97.1 percent) of haplotype variance was among populations and only 6 percent (2.8 to 9.3 percent) was attributable to trees within populations. The distribution of haplotypes in California suggested about four major groups (*fig. 1*). 1) The San Francisco Bay Area and northwards, haplotypes 1, 6 and 30 are common. Of these, only haplotype 6 is found outside of this region at York Mountain Road in San Luis Obispo County and at Ojai in Ventura County. 2) In the Monterey-Big Sur region, haplotype 17 is common and 16 and 21 are also present. These haplotypes are not found elsewhere. 3) In the coastal mountains of San Luis Obispo County, haplotypes 2 and 28 are unique, haplotype 6 is shared with the north and haplotype 27 is shared with more interior populations near Parkfield. 4) In extreme Southern California, six haplotypes were detected with only one (haplotype 8) being detected outside of this region at Ojai and Lebec in Ventura County. The populations from Baja California, Mexico, did not share any haplotypes with sample sites further north. Extreme interior populations at Pacheco State Park and Cordelia had unique haplotypes, suggesting that recent gene flow by seed from more coastal populations has not penetrated these areas.

Figure 1—Distribution of 31 chloroplast haplotypes of coast live oak. Sequence of numbers does not represent haplotype evolution.

The BARRIER analysis detected five major barriers to gene flow (*fig. 2*). The first and most important of these divides populations into a southern and a northern group along a line between Ojai to Lebec and the San Gabriel Mountains. The second most important barrier separated interior population Parkfield. The third and fifth barriers occurred in Baja California, Mexico, indicating relatively high differentiation among these most southerly populations. The fourth barrier separated populations from the central California coast from those further north and east.

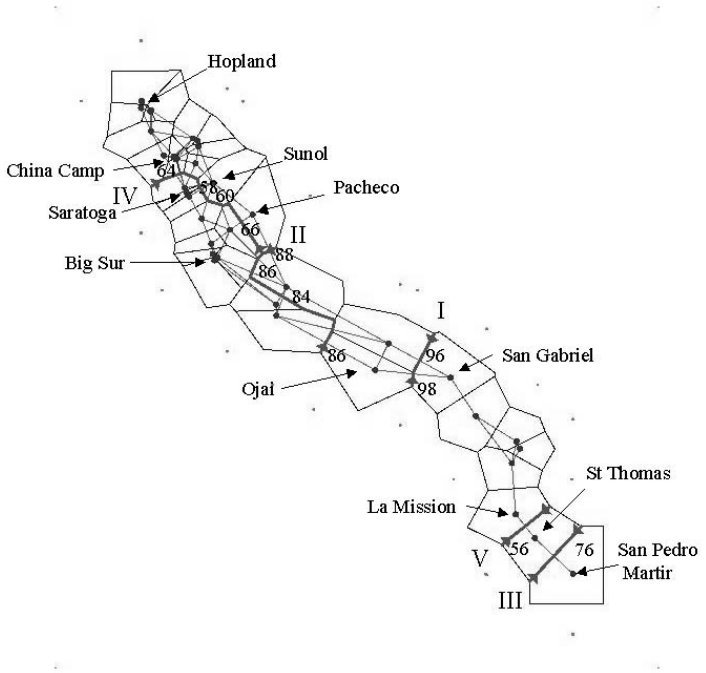

Figure 2—Barrier analysis for coast live oak based on chloroplast microsatellites. Barriers shown as thick lines and numbered in order of importance are derived by combining a genetic distance matrix with Delaunay triangulations (fine lines) derived from Voronoi tessellations (polygons) around sampled populations (dots). Bootstrap support by re-sampling 100 subsets within populations shown for each barrier segment.

Nuclear DNA

Analysis of molecular variance revealed a much lower level of population differentiation for nuclear DNA than for chloroplast DNA: 23 percent (95 percent confidence limit 17.9 to 28.6 percent) among populations and 77 percent (69.8 to 85.1 percent) within populations.

Seven significant barriers were detected among the 28 populations (*fig. 3*). The first, most significant of these was in Northern California, separating populations north of northern Marin County from all populations further south. The second barrier separated interior population Pacheco, which was concordant with the analysis of chloroplast DNA. The third barrier separated the central California coast population from Big Sur. Although this was also generally concordant with the chloroplast structure, more limited sampling for nuclear DNA along the coast northwards to the San Francisco Peninsula precludes inference of the extent of this partition based on nuclear DNA. The fourth and fifth barriers were also in Northern California, separating the northernmost population from Cloverdale and the interior population of Morgan respectively. The sixth barrier separated Lebec from Ojai and populations further south. The final significant barrier occurred in Southern California between populations from San Diego County and El Cariso on the Cleveland National Forest in Riverside County.

Discussion

Overall population differentiation based on chloroplast markers was high in coast live oak, consistent with a maternally inherited marker and suggesting that the heavy seeds of coast live oak are dispersed over relatively short distances. The distribution of chloroplast haplotypes in Figure 1 suggests four major biogeographic groups. The barrier analysis indicates a most significant north-south split between the southernmost limit of the outer south coast ranges (sensu Hickman 1993) and the San Gabriel Mountains of the Transverse Ranges. However, populations from Ojai and Lebec shared one haplotype with some populations from Northern California and another with populations from Southern California, suggesting a possible transitional region of admixture of northern and southern groups. It will be interesting to sample more intensively in this region to detect more precisely where the *cp*DNA break occurs. The other *cp*DNA biogeographic regions supported by barriers included central coast populations, populations from the San Francisco Bay and northern coast ranges, interior populations and the extreme southern populations from Baja California, Mexico. Topography may explain these breaks, but more intense sampling to confirm this is necessary. For example, the haplotype map suggests a central coast group extending through the Santa Lucia Mountains to the Monterey Bay, whereas the barrier analysis extends this group north to the San Francisco Peninsula. It is therefore unclear whether the Salinas Valley, or the San Francisco Bay is the effective barrier to the dispersal of seed in this region. Our sampling was more intensive in Northern California, and we intend to sample more populations in the southern range to confirm our preliminary data.

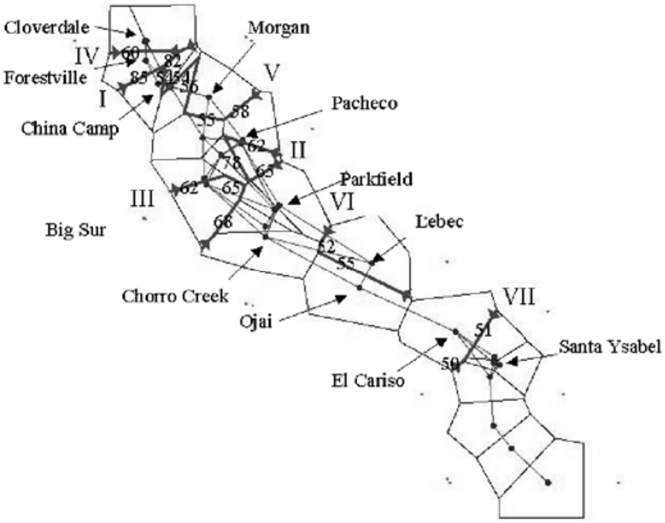

Figure 3—Barrier analysis for coast live oak based on nuclear microsatellites. Barriers shown as thick lines and numbered (roman numerals) in order of importance are derived by combining a genetic distance matrix with Delaunay triangulations (fine lines) derived from Voronoi tessellations (polygons) around sampled populations (dots). Bootstrap support by re-sampling 100 subsets within populations shown for each barrier segment.

As expected for an outcrossing, wind-pollinated species, the level of population differentiation based on nuclear DNA was much lower than that of *cp*DNA. The partition of population genetic structure based on nuclear DNA was only partially concordant with that based on *cp*DNA. It has often been noted that these two marker systems show conflicting patterns in oaks, with *cp*DNA variation among sympatric species or populations depending more on geography than on phylogenetic relationships (Whittemore and Schaal 1991, Dumolin-Lapégue and others 1999). The nuclear DNA results supported the *cp*DNA data in identifying the Central Coast and the interior populations as forming distinct groups. However, contrary to the *cp*DNA results, there was more intense population differentiation based on nuclear DNA in Northern California than in the south. Genetic diversity as measured by allelic richness was also highest in two of the northernmost populations in California. Earlier studies have shown that hybridization between coast live oak and interior live oak is more prevalent in Northern California (Dodd and others 1993, 2002, Dodd and A.-Rafii 2003) and this may partially explain the discordant patterns of population differentiation based on the two marker systems. Elsewhere, we have shown that the most common chloroplast haplotype for coast live oak in Northern California is likely to be a haplotype of interior live oak (*Quercus wislizeni* A. DC.) and it can be detected in populations of this latter species throughout Northern California beyond the range of coast live oak (Dodd and others 2005). It would appear that pollen swamping from coast live oak results in hybrid progeny that have captured the maternally inherited *cp*DNA of interior live oak. Subsequent backcrossing of these hybrid progeny to coast live oak results in coast live oak phenotypes with interior live oak chloroplast genomes. In populations of interior live oak over much of north-western California, the haplotype appears to be fixed, so that coast live oak resulting from hybridization through pollen would also carry a fixed haplotype. In contrast to the chloroplast genome, hybridization should result in the incorporation of the nuclear genome of both species. Whereas backcrossing may dilute the genome of one parent, it will nevertheless persist over many generations. Thus in a region of pollen swamping, nuclear diversity should be relatively high. Similar effects of pollen swamping have been found in *Eucalyptus* (Potts and Reid 1988, Potts and others 2003) and in European oaks (Petit and others 1997, Belahbib and others 2001). Hybrids between coast live oak and Shreve oak have been detected from multilocus genotypes (Dodd and Rafii 2003) and chloroplast sharing between these two species in central coastal California was also detected here, but we were unable to determine directionality.

Compared with other oak species, we have detected relatively high genetic structure among populations based on chloroplast and nuclear DNA. It would be most interesting to evaluate whether this translates equally to transcribed genes that control traits of ecological importance. It is encouraging that hybridization with interior live oak appears to be facile in Northern California where summer temperatures are predicted to increase more than in the southwest (Hayhoe and others 2004). Whereas coast live oak is adapted to a Mediterranean climate under the influence of summer fog, interior live oak is better adapted to more continental conditions of drought and extreme temperatures. Hybrid products between these two species may offer genotypes that will be well-adapted to the new ecological conditions. Concerning disease resistance, our earlier studies were equivocal regarding possible population variation in lesion size after inoculation with *Phytophthora ramorum.* In spring inoculations, we detected significantly smaller lesions in branch cuttings from populations from southern California compared with Northern California, but this difference was not replicated in summer inoculations (Dodd and others 2005). We are currently testing whether this could be a seasonal effect.

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Continue

Incorporating Genetic Information Into Conservation Planning for California Valley Oak[1]

Victoria L Sork,[2] Frank W. Davis,[3] and Delphine Grivet[2]

Abstract

Many plant species are of sufficient ecological importance to merit species-specific conservation plans. For species threatened by land use change, protected areas will be a key element of their conservation strategy. It can be particularly challenging to identify which sites to preserve for broadly distributed species such as California valley oak (*Quercus lobata* Née) that possess geographically structured genetic variation. Here, we investigate the use of molecular markers to identify populations of high genetic diversity or high genetic uniqueness for designing a network of protected areas. In an earlier study, we sampled individuals from 32 valley oak populations distributed throughout the species range and determined their genotypes based on chloroplast haplotypes (six primers) and nuclear genetic markers (seven primers). Our findings from that study indicated a north-south gradient in genotypes and significant genetic differences between western and eastern populations. For this paper, we analyzed the data from a reserve design perspective. We conclude that a minimum of six of 32 locations would be needed to represent genetic variation as indicated by chloroplast DNA and at least 10 of 37 locations would be required to represent genetic variation as indicated by allelic variation in nuclear DNA. The analysis suggests that an efficient reserve network for protecting genetic variation in the species can be developed by including sites of high allelic diversity that are also complementary in their allelic composition. Many factors need to be considered in locating reserves, notably site biotic composition and condition, threatening processes, cost, and opportunity. Incorporating genetic information enhances the description of site composition, providing a historical evolutionary perspective.

Keywords: Biodiversity, conservation plan, genetic diversity, Quercus, *reserve design.*

Introduction

Biological diversity is manifested at many spatial scales and at many levels of organization, ranging from landscapes comprised of multiple ecosystems and species populations to genotypes within individual species (Noss 1990). Conservation planning in California and elsewhere has increasingly focused on landscape-scale, multi-species conservation (Groves and others 2002). At the same time, conservation biologists recognize the need to preserve genetic diversity within individual species, often by protecting populations in different parts of a species' range (Lomolino 2006). Conservation genetics has tended to focus on threatened or endangered species or species of commercial importance. For example, the Endangered Species Act includes a provision for listing "distinct population segments" of vertebrates, and the National Marine Fisheries Service has adopted the concept of "evolutionarily significant units" (ESUs) in designing conservation strategies for Pacific salmon

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[2] Department of Ecology and Evolutionary Biology, and Institute of the Environment, University of California, Box 951606, Los Angeles, CA 90095-1606..

[3] Donald Bren School of Environmental Science and Management, University of California Santa Barbara.

species (Waples 2006). Additionally, it has provided a good vehicle for the preservation of plant species (Holsinger and Gottlieb 1991). Similarly, we would argue that it is important to consider genetic variation in devising conservation strategies for oak species that define California's threatened foothill oak woodland ecosystems.

In this paper, we focus on the use of genetic data for informing conservation planning for valley oak (*Quercus lobata* Née). Valley oak woodlands have been extensively converted and fragmented by agricultural and urban development (Pavlik and others 1991). Perhaps one-third of Valley oak savanna remains from its pre-European settlement distribution (Davis and others 1998). In the San Joaquin Valley roughly 95 percent of the riparian valley oak forest and valley oak woodland have been removed (Kelly and others 2005). Moreover, existing populations are experiencing significant loss of recruitment (Bolsinger 1988, Brown and Davis 1991, Tyler and others 2006). Conserving the ecological and evolutionary potential of valley oak will require habitat protection and restoration, attention to connectivity among fragmented sites, and enhancement of demographically viable local populations. An additional component of an effective strategy for valley oak will be a network of protected areas that is designed to conserve genetic diversity.

Several approaches are available for the use of genetics in reserve design. Based on Fisher's (1930) principle that the amount of genetic variation is related to the evolutionary potential of a population, many conservation biologists emphasize the importance of maintaining genetic variation within and among populations (Ledig 1988, Frankham and others 2002). Most conservation strategies have used neutral markers as a surrogate of population evolutionary potential, but some biologists caution that assessment based on neutral genetic markers might overlook more important adaptive genetic variation (Lynch 1996, Reed and Frankham 2001). This concern is valid, and both molecular variation and adaptive traits can be integrated in conservation strategies, each of them providing complementary information (Toro and Caballero 2005). However, several limitations (e.g., cost, use of the appropriate molecular markers, development of statistical tools) hamper the use of adaptive markers in conservation (Luikart and others 2003, Gonzalez-Martinez and others 2006). A phylogeographic approach to reserve network design has been advocated to maximize genetic diversity and to retain populations representing the evolutionary history of the species (Moritz 1994, Avise 2000, Crandall and others 2000). Moritz (1994) argues that ESUs based on the organelle genome, such as mtDNA, would indicate appropriate management units for conservation. Newton and others (1999) counter that the ESU approach to tree populations, using chloroplast markers, should be used with caution because phylogeographic studies may not always be ideal for conservation problems due to interspecific gene exchange in trees. Instead, they recommend that management units (MUs) based on nuclear genetic differences might be more informative. Meanwhile, several authors point out other limitations to the use of the ESU approach (Paetkau 1999, Avise 2000, Crandall and others 2000, Fraser and Bernatchez 2001). In sum, there is not yet consensus on the best way to obtain genetic data and incorporate it into land use planning (Moritz and Faith 1998).

In a separate paper, we applied a geographical genetic approach to valley oak. In that study, we conducted a multivariate analysis based on chloroplast and nuclear microsatellite genotypes to create a canonical trend across the species' range in order to test for geographical pattern of the genetic data (Grivet and others 2008). Multivariate genotypes provide sensitive measures of genetic differences among populations (Westfall and Conkle 1992, Kremer and Zanetto 1997). The fact that they have been effectively used to identify seed zones in forestry suggests that at least some of those genetic differences are surrogates for adaptive genetic variation. In that paper, we identify geographic genetic trends in both the chloroplast and nuclear markers. Our findings show significant genetic differences on a north/south transect reflecting strong genetic differences across the species range. We also identify areas of sharp genetic gradients that are suggestive of high evolutionary interest and warrant more intensive sampling for future work.

Here, we use the genetic data described above to explore strategies for conserving genetic diversity in valley oak. We apply a “set covering algorithm” to identify the minimum number of locations needed to represent the allelic diversity documented at our sampling sites, as well as to measure how much diversity could be captured at a smaller number of locations by exploiting patterns of allelic richness and complementarity in allelic composition of different sites (Margules and Pressey 2000). We analyze both chloroplast and nuclear microsatellite alleles throughout the species range. By using the chloroplast markers, we incorporate longer-term evolutionary history into our analysis because the chloroplast is maternally inherited (Dumolin and others 1995) and its DNA is very conservative (Wolfe and others 1987). Specifically, we will ask the following questions: (1) How many sites are needed to represent *Quercus lobata* allelic diversity based on (a) chloroplast DNA, (b) nuclear DNA, and (c) both markers combined? (2) How are these sites distributed geographically? (3) How irreplaceable are sites in assembling a representative reserve network for valley oak genetic diversity? (4) Are there efficiencies in targeting certain areas based on patterns of allelic richness and complementarity?

Methods

The study species, *Quercus lobata* Née, is a California endemic tree species. It mainly occurs in closed riparian forests of the Central Valley and at lower density in woodlands and savannas in low-elevation valleys and foothills of the Sierra Nevada, Coastal Ranges, and Transverse Ranges (Griffin and Critchfield 1972). Because of their extended latitudinal distribution (34-40˚ latitude) and the complex topography of California, *Q. lobata* populations are spread across various climatic and geographic regions. Valley oak is wind-pollinated and essentially 100 percent outcrossing (Sork and others 2002b). Dispersal agents include acorn woodpeckers, scrub jays, squirrels, and smaller rodents. Our laboratory has been involved in a series of genetic studies investigating contemporary pollen movement (Smouse and others 2001, Sork and others 2002a, Sork and others 2002b), contemporary acorn movement (Grivet and others 2005) and fine-scale genetic structure (Dutech and others 2005). Collectively, these studies of contemporary and recent historical gene flow indicate that the scale of dispersal determining a genetic neighborhood is ca 100 to 300 m, but these estimates do not preclude occasional long distant pollen or seed dispersal.

The data used for this paper were collected in 2003 and 2004 as part of an ongoing genetic analysis of the biogeographical patterns of California valley oak (Grivet and others 2006; Grivet and others 2008). We mainly sampled valley oaks in oak woodlands and savannas in foothill environments around the Central Valley as opposed to oaks in remnant gallery forests of the Central Valley floodplains. We sampled 37 populations with three to four individual trees per site for a total of 113 individuals (*fig. 1, table 1*). The chloroplast (cp) data set includes 32 populations and

97 individuals (*table 1*). The methods of DNA extraction as well as PCR conditions are described in Grivet and others (2006). These samples were genotyped for six chloroplast microsatellites: ccmp10 was designed from *Nicotiana tabacum* DNA (Weising and Gardner 1999), while µdt1, µdt3, µdt4, µcd4, and µcd5 were designed from *Quercus robur* DNA (Deguilloux and others 2003).

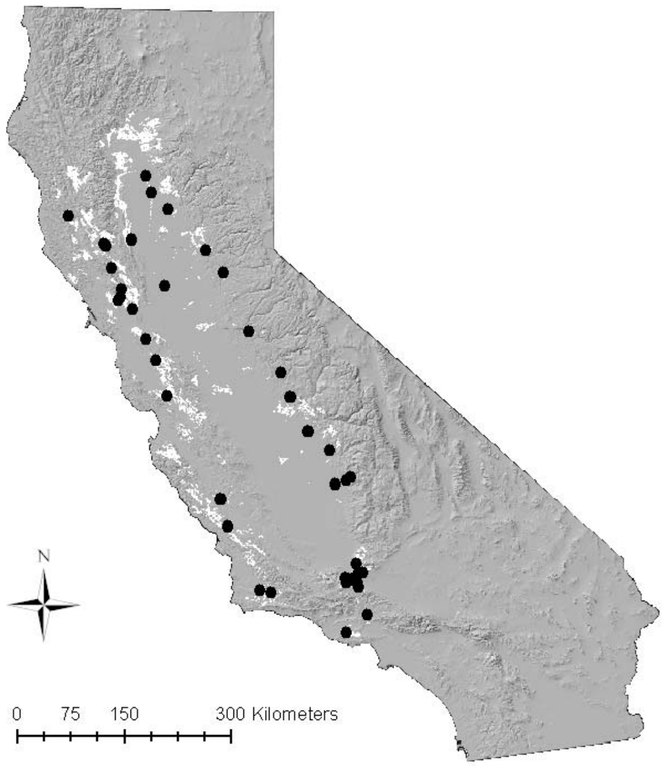

Figure 1—Location of 37 sampling sites for California valley oak (*Quercus lobata*). White regions indicate contemporary distribution of valley oak.

The nuclear (n) data set includes 113 individuals from all 37 populations (*fig. 1*; *table 1*). The methods for DNA extraction and PCR conditions are described in Grivet and others (2008). We used seven nuclear microsatellites: MSQ4 (Dow and others 1995), QpZAG1/5, QpZAG9, QpZAG36, QpZAG110 (Steinkellner and others 1997), QrZAG11, and QrZAG20 (Kampfer and others 1998). We measured the length of the amplified sequence by running an aliquot of each PCR product on an ABI 3700 capillary sequencer at the UCLA Sequencing & Genotyping Core Facility (http://www.genetics.ucla.edu/sequencing/index.php). To check repeatability, each sample was re-genotyped, after repeating the PCR reactions.

Table1: characterization of valley oak populations (n = 37). Each population is characterized by three individuals, except for populations 37 and 55 that have four individuals. Populations in bold were analyzed for nuclear markers only.

Population ID	Latitude (decimal degrees)	Longitude (decimal degrees)	Elevation (meters)
1	34.8156	-118.8251	1201
2	36.0479	-119.0344	138
3	36.0979	-118.8654	216
4	36.1122	-118.8440	320
5	36.4850	-119.1205	153
8	36.7253	-119.4596	118
9	37.1534	-119.7341	359
10	37.4619	-119.8798	656
11	37.9798	-120.3884	537
13	38.7139	-120.8115	539
14	38.9963	-121.1085	453
16	39.4984	-121.7289	44
17	39.7115	-122.0043	43
25	39.3836	-123.3433	450
26	39.0364	-122.7402	427
27	39.1068	-122.3079	127
28	38.7476	-122.6186	332
29	38.4831	-122.4434	58
30	38.2392	-122.2675	19
31	37.8646	-122.0346	77
32	37.6018	-121.8731	84
33	37.1556	-121.6904	295
34	35.8679	-120.8211	129
35	35.5275	-120.7039	221
36	34.7231	-120.2160	239
37	38.5351	-121.7494	18
40	38.3538	-122.4817	73
42	39.9094	-122.0897	58
45	34.8742	-118.8948	988
46	34.4099	-118.5741	359
47	34.1871	-118.8909	202
48	34.6963	-120.0401	337
49	34.7548	-118.7095	1119
50	34.8451	-118.8302	1088
51	34.9173	-118.7169	1536
52	34.9416	-118.6321	1409
55	35.0520	-118.7340	406

For the cpDNA data set, we documented 22 total alleles across six microsatellite loci. For the nuclear DNA data set, we catalogued 78 alleles from seven microsatellite loci. For the set covering analysis, each sample site was characterized by the presence or absence of each allele. We used MARXAN 1.8 reserve design software to identify sets of sites that captured the greatest number of alleles for a specified set size, as well as the minimum number of sites needed to satisfy the goal of representing every allele at least once in the final set (Possingham and others 2000). We used the simulated annealing search option, a stochastic search procedure that iteratively creates and compares sets of sites and selects the set that best achieves the specified conservation targets at the lowest cost. Here we set a target of representing each allele at least once in the final set. All sites were assigned an arbitrary equal cost and all alleles were weighted equally. We assumed that all sites were unprotected unless selected and also ignored site differences in threat from future landscape change. MARXAN 1.8 also allows spatial design parameters (e.g., clustering of sites) but we did not include any spatial weighting. We selected the best set for site networks ranging in size from one site to as many as needed to represent all alleles by varying cost and penalty functions (see Possingham and others 2000). For each network size, we selected the best set from 100 model runs of 1 million iterations each. We first analyzed the chloroplast and nuclear datasets separately and then we examined the pooled data for sites where both cpDNA and nDNA were sampled (n = 32).

Results

Out of 32 sites with cpDNA data, site 31 has the highest allelic richness and represents 12 of 22 alleles. Twenty of 22 alleles can be represented with three of the 32 sites indicating that there are other high-diversity sites that are relatively complementary in their composition. To represent all 22 alleles, including three rare alleles that occur at only one site each, requires six sites. One site (27) is irreplaceable and four sites (sites 27, 25, 33, 46) appear in more than half of the best set of solutions (*fig. 2*). These sites are all found in the western range of the species distribution and most of them in the north (*fig. 2*).

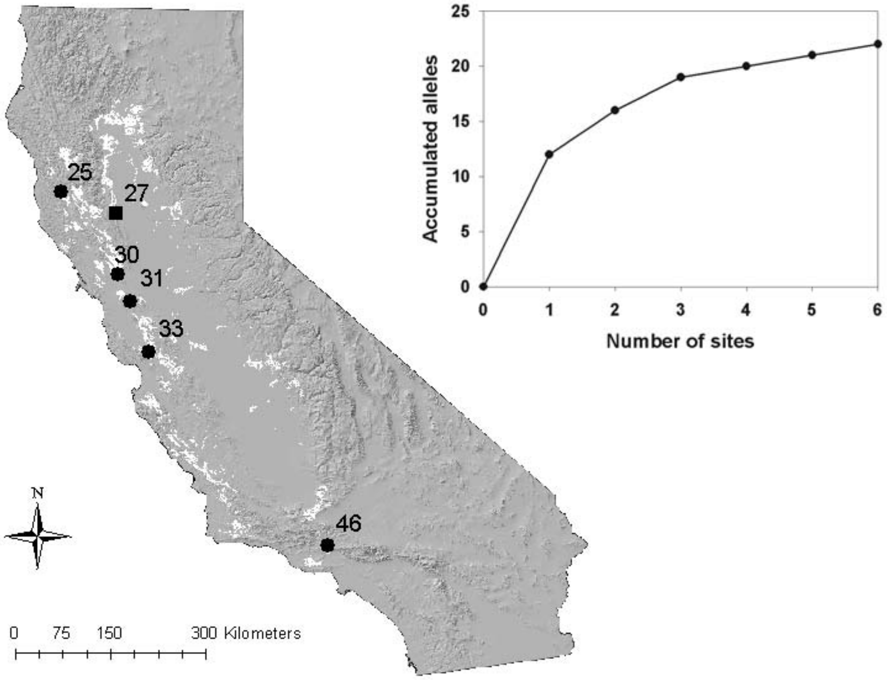

Figure 2—Map of set of **six** sites that captures most of the **chloroplast** allelic diversity in *Quercus lobata*. Squared symbols represent irreplaceable sites. Embedded chart indicates accumulation of chloroplast alleles.

For the nDNA alleles, 10 sites are required to obtain complete coverage of 78 alleles (*fig. 3*). The accumulation curve is steep at first, indicating the occurrence of rich and complementary sites. The last additional sites are needed to capture rare alleles. Three sites are perfectly irreplaceable (sites 52, 48, and 47 occur in all 100 solutions) and are locally distributed (all are in the South-West) (*fig. 3*): one in the Tehachapi Range, one in the Santa Inez Valley, and one in the Southwest, respectively. In contrast to the cpDNA analysis, the sites needed for full representation of nDNA are distributed throughout the range of valley oak (*fig. 3*), with a slight bias towards sites in the southern part of the range.

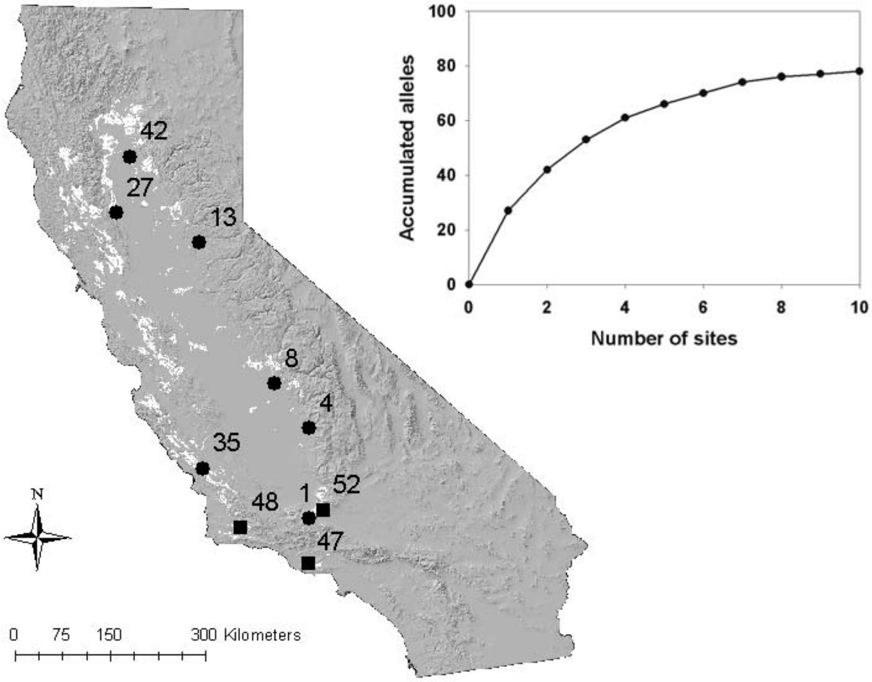

Figure 3—Map of set of **10** sites that captures most of the **nuclear** allelic diversity in *Quercus lobata*. Embedded chart indicates accumulated nuclear alleles.

To evaluate reserve design based on the combined markers, we used 32 populations and 100 total alleles. In this final analysis, 11 sites are required for a complete solution and two sites capture more than 50 percent of the alleles (*fig. 4*). Solutions with at least six sites capture all chloroplast alleles and most nuclear alleles. We found two sites to be perfectly irreplaceable (*fig. 4*): one in the Sierra foothills (13) and one in the San Inez Valley (48). The 10 sites occurring most often in the solution to capture most of the alleles are distributed through the entire species range (*fig. 4*). Generally the solution for cpDNA can be nested inside the solution for nDNA.

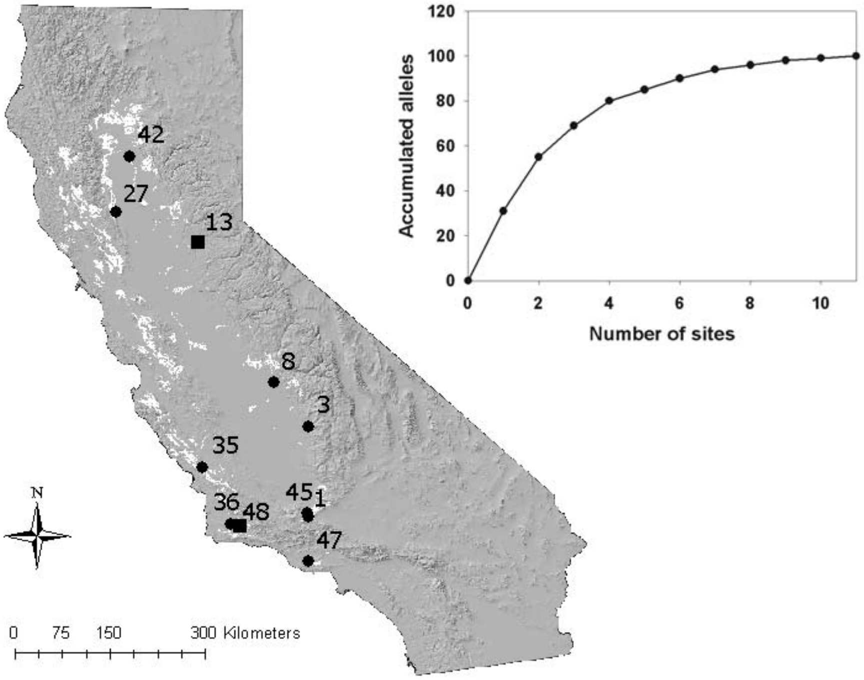

Figure 4—Map of set of **11** sites that captures most of the allelic diversity when pooling chloroplast and nuclear microsatellite alleles. Embedded chart indicates rate of accumulation.

Discussion

Many factors must be considered in designing biodiversity reserve networks in the real world, notably social goals, the quality and condition of biological resources, threats, costs and opportunities (Prendergast and others 1999, Davis and others 2006). Representation of existing diversity is a basic goal of systematic conservation planning (Margules and Pressey 2000). Without considering the many other dimensions of reserve network design, we have analyzed valley oak genetic data to explore what a representative network of sites to protect genetic diversity in valley oak might look like in terms of number of sites, geographic distribution and site irreplaceability.

Our results are preliminary because we would like to sample more individuals per site and more sites, especially in under-sampled regions and environments such as the gallery forests of the Sacramento and San Joaquin river basins and in areas identified by Grivet and others (2008) as having sharp genotypic gradients. Moreover, our sample design (i.e., few individuals per population) is appropriate for chloroplast markers because they present a low level of genetic diversity within most of the sites, but it would be preferable to include more nuclear genotypes per site for the interpretation of the nuclear results. With these caveats, these findings based on a widely distributed set of populations present a useful analysis of a reserve design network for valley oak. It appears that a representative network will necessarily require distributing sites across the geographic distribution of the species. The number of sites will depend on whether the system is designed to exploit efficiencies obtained through selection of areas that have high diversity and are also complementary in composition to other sites. The steep accumulation curves for both cpDNA and nDNA argue in favor of such a systematic approach. It also appears that a network design based on cpDNA will differ from that based on nDNA markers, possibly because one set is more based on colonization history and the second is the outcome of multiple evolutionary pressures. This finding supports the recommendation of Fraser and Bernatchez (2001) to utilize more than one kind of genetic information. The combined analysis is a good way of developing a reserve design that integrates the two sets of genetic markers, and, in this study, it seems that we can preserve much of the cpDNA diversity within the sampling scheme for the nDNA markers. The current analysis constitutes the first step in designing a network by incorporating neutral markers from two genomes with different evolutionary histories. Future work should include more sites, especially in ecosystems that we have not yet sampled such as riparian forests, as well as more individuals per site. Moreover, it would be valuable to include genes that are linked to adaptive traits, although such loci are not yet available for *Q. lobata*.

It is reassuring that the interpretation based on a very simple genetic model of simply maximizing genetic variation across the species range captures the areas of genetic interest that we identified in our multivariate genetic approach (Grivet and others 2008). In that paper based on the same sets of data, we found a latitudinal gradient of chloroplast and nuclear multivariate genotypes, with genetically distinct northern and southern areas. Based on those patterns, we advised that it appears that there would be a need for more reserves in the north and in the south when taking into account both markers, but we did not translate that interpretation into a reserve design. Here, we use a formal reserve design approach with simple assumptions of allelic sampling and arrive at similar conclusions.

To compare the reserve solution observed here with that based on a phylogeographic approach, it will be necessary to use DNA sequence data for multiple genes of valley oak. Such work would be costly but it would yield an effective scrutiny of analyses based on microsatellite data. In addition, it would present a more precise genetic history of valley oak, both for its own sake, and it would reveal whether the set covering solution is capturing evolutionary lineages and history. If so, future studies could deploy a molecular approach to reserve design based on the less expensive allelic approach rather than a sequence approach.

The next step in modeling the analysis of reserve design, once we have more data, would be to incorporate other factors that influence decision-making around site selection (Davis and others 2006). Before setting conservation priorities simply based on the biological analysis, it would be practical to consider the value of a site based on resource quality, threats to resource quality, and costs. For example, threats to resource quality are of major concern in California. An analysis of site vulnerability to land conversion indicates that almost the entire distribution of valley oak is in areas of high vulnerability to land conversion (Davis and others 1998). Future work would yield much more practical results if it integrated both biological and socioeconomic considerations. Our preliminary analysis indicates some flexibility in site location, and California has enough extant populations that reserve design could take into account these other factors. However, the choice of sites will decline with time and critical areas from a genetic standpoint could be lost as well.

Finally, we point out that a robust reserve design will need to account for other factors associated with site quality such as proximity to other populations outside the "reserve." Lack of connectivity and/or small population size could result in loss of genetic diversity within the reserve. Ongoing studies in our laboratory are attempting to understand gene flow within and among fragments that could help assess resource quality of a habitat based on this process.

Valley oak is a significant element of California's biodiversity that is threatened by landscape change and population attrition. Public agencies and private organizations like The Nature Conservancy and the California Oak Foundation are already engaged in many conservation and restoration efforts throughout the range of the species. Due to the habitat importance of valley oak, a preservation plan is likely to include far more sites than those needed to preserve genetic and evolutional processes. Nonetheless, a systematic analysis of genetic diversity in existing and candidate reserve sites using the kind of tools demonstrated here could help to more fully characterize the current network of protected areas and help these organizations prioritize future investments in conservation and restoration projects.

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Continue

Net Primary Production and Biomass Distribution in the Blue Oak Savanna[1]

John J. Battles,[2] Randall D. Jackson,[3] Ayn Shlisky,[4] Barbara Allen-Diaz,[2] and James W. Bartolome[2]

Abstract

The complexity of savanna ecosystems with the shared dominance between woody and herbaceous primary producers poses challenges to measuring such fundamental ecosystem characteristics as net primary productivity (NPP). We address these challenges in the blue oak savanna in California by constructing comprehensive estimates of NPP for three adjacent watersheds. We directly assessed annual biomass increment of all plant components in 12 randomly stratified plots (380 m^2) per watershed. Annual estimates of mean NPP for the three experimental watersheds during 2001 to 2002 ranged from 4.35 to 5.69 Mg ha^{-1} yr^{-1} of dry biomass. On average, belowground NPP accounted for 22 percent of total NPP. In general, there was much greater uncertainty in the belowground estimates. Trees accounted for approximately 50 percent of aboveground NPP in all three watersheds. Across these watersheds, tree productivity increased in a linear fashion with canopy closure. In contrast, herb productivity was nearly constant for relatively open sites (canopy closure < 40 percent) and then monotonically declined as canopy closure increased. The result is that total NPP increased gradually from the most open sites in the watersheds to a maximum around 55 percent canopy closure.

Keywords: Biomass distribution, carbon budget, Mediterranean ecosystem, net primary production, temperate savanna.

Introduction

A fundamental characteristic of savanna ecosystems is the co-dominance of tree and grass life forms. Savannas and synonymous designations (e.g., woodland, rangeland, shrubland) constitute a gradient of ecosystems that fall between grasslands and forests. Together they account for more than an eighth of the terrestrial biosphere (Scholes and Archer 1997). They are economically and ecologically important in tropical and temperate regions throughout the world. Despite their extent and value, basic ecosystem functions of savannas are poorly understood relative to grasslands and forests.

In a recent review, House and others (2003) noted that challenges to developing a robust understanding of savanna ecosystems included a preponderance of studies that focused on either the grass or tree component in isolation and a lack of studies that addressed belowground productivity and biomass. Yet it is this sort of integrated ecosystem-level information that is crucial to understanding savanna dynamics and to

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[2] University of California, Berkeley, Department of Environmental Science Policy and Management, 137 Mulford Hall, Berkeley, CA 94720-3114.

[3] University of Wisconsin-Madison, Department of Agronomy, 1575 Linden Drive, Madison, WI 53706.

[4] The Nature Conservancy, 2424 Spruce St., Boulder, CO 80302.

managing them appropriately. In this paper, we summarize our efforts to confront these challenges for the blue oak savanna in California.

A critical management objective in California oak savanna is to sustain livestock productivity while maintaining long-term ecosystem health. Despite a wealth of information regarding the productivity of certain components of this ecosystem including forage yield (Holland 1980, Kay 1987, Connor and Willoughby 1997), leaf and acorn production (Dahlgren and Singer 1994, Knops and others 1996, Koenig and others 1996, Koenig and others 1999), fine root growth (Jackson and others 1990, Millikin and Bledsoe 1999), and tree growth (Kertis and others 1993), there exists no estimate of total net primary productivity (NPP). Without NPP estimates, we cannot address basic ecological questions about NPP allocation under various biotic and abiotic scenarios–information that is useful for predicting the effects of land-use modifications or climate changes on C cycling and plant community distribution. Moreover, in savannas where NPP has been estimated, there exists what House and others (2003) describe as the “NPP conundrum”–competing hypotheses about the nature of NPP allocation between trees and herbs as tree dominance varies.

The general relationship noted by House and others (2003) is for declining grass NPP with increasing tree dominance where dominance is measured as a function of tree density, basal area, or canopy cover. Robust tests of this relationship remain rare, though Reich and others (2001) found that aboveground NPP decreased with increasing tree dominance in oak savanna of the upper Midwest supporting this relationship. Alternatively, Mitchell and others (1999) reported that in the pine-wiregrass savanna of the southeastern United States, the highest grass productivity occurred at sites with the greatest tree density.

In the blue oak savanna, several studies have concluded that the presence of trees enhances understory productivity (Callaway and others 1991, Dahlgren and others 1997) primarily due to processes associated with nutrient cycling. However, results from tree removal studies conflict (Connor and Willoughby 1997). For example, experiments conducted at the same research station in the blue oak savanna have drawn opposing conclusions (Holland 1980, Kay 1987).

In 2001, we initiated a study to explore the patterns in productivity and the distribution of biomass in the blue oak savanna. We will use this information to develop a measure of ecosystem health, based on a robust and integrated estimate of NPP for an entire management unit (i.e., the watershed). We measured NPP across the grass-tree mosaic using techniques from landscape and community ecology to efficiently allocate our sampling effort and to properly extrapolate our plot-level results. Specifically, our objectives were to produce watershed-level productivity and biomass budgets for blue oak savannas and to examine the internal relationships between productivity and tree abundance in the blue oak savanna.

Methods

Study Site

In 2001, we identified three adjacent watersheds and instrumented them to measure NPP. The experimental watersheds are located in the foothills of the northern Sierra Nevada at the University of California Sierra Foothill Research and Extension Center (SFREC) near Marysville, CA. (39º 15' N, 121º 17' W). These three adjacent watersheds, collectively known as the Lewis watersheds, contain hilly, rolling terrain.

They range in size from 35 ha (WS1) to 116 ha (WS3) and encompass an elevation gradient from 189 to 584 m.

The climate is Mediterranean with cool, wet winters and hot, dry summers. Based on the onsite weather records for the past 15 years (California Irrigation Management Information System, Browns Valley Station #84, http://wwwcimis.water.ca.gov/cimis), total annual precipitation ranges from 49 to 133 cm with a mean of 77.5 cm. Most of the rain (98 percent) falls between October and May. There is a prolonged summer drought (June-September) where relative humidity averages less than 45 percent and mean daily air temperature is 24°C. Annual estimates of productivity coincide with the water year, which starts on October 1, the typical beginning of winter rains, and ends the following September 30. Thus, the estimates reported here for 2002 include all the plant production that occurred during the 2002 growing season, even though the year began on October 1, 2001.

Soils within the watersheds formed in basic metavolcanic (greenstone) bedrock. They are classified as fine, mixed, thermic Typic Haploxeralfs (Dahlgren and others 1997). These soils can extend to a depth of 100 to 150 cm and overlie relatively massive bedrock.

The vegetation of the foothills consists of an overstory dominated by the winter-deciduous blue oak (*Quercus douglasii*). Interior live oak (*Quercus wislizenii*) and foothill pine (*Pinus sabiniana*) are present at lower densities (Shlisky 2001). As is typical for savanna ecosystems, the trees are patchily distributed across the landscape. Canopy cover varies from less than 4 percent to more than 80 percent with a watershed-level mean of 56 percent. Based on the 2002 inventory, the three most common plants in the grass-dominated understory (42 percent cover) are the introduced annual grasses: *Bromus hordeaceus, Bromus madritensis* and *Cynosurus echinatus*. The next most common species (8 percent cover each) are the introduced annual forbs, *Trifolium hirdum* and *Torilis nodosa*. Common shrubs include poison oak (*Toxicodendron diversiloba*) and coffeeberry (*Rhamnus californica*). The prevailing management regime in these watersheds includes fire exclusion and grazing at moderate intensity by a cow-calf herd in the green season (December through May). In 2002, herbivore consumption (domestic and native) on the grass layer was approximately 0.37 Mg yr^{-1} (22 percent of grass productivity).

Data Collection and Analysis

Productivity sampling was based on the stratified random design described in Shlisky (2001). Using color aerial photographs, watersheds were divided into four tree-cover classes (<15 percent, 15 to 30 percent, 30 to 60 percent, and >60 percent). The minimum mapping unit was 2 ha. Sampling intensity in each watershed was allocated to each cover class proportional to its abundance. Plot locations were randomly assigned in each cover class. From this set of 64 plots, we randomly choose a subset of 36 locations to establish NPP plots (3 per strata, 12 per watershed). Note that all watershed-level estimates (means and variances) were weighted by the proportional abundance of the cover class in the watershed (Cochran 1977).

NPP plots consist of an 11-m radius circular area (380 m2). Shlisky (2001) demonstrated that plant composition and canopy structure is relatively homogeneous at this scale. In 2001, all live trees ≥ 5 cm diameter at breast height (1.37 m, dbh) within the plot were identified, measured, and tagged. Dendrometer bands were installed on a size-stratified subset (15 percent of total, 94 trees) of these trees in order to measure annual stem increment.

Within each plot, three "cattle-resistant" litterfall traps were systematically placed at 3, 5, and 7 m from the center at 120° angle from each other. These traps were approximately 1.5 tall to avoid disturbance from cows. The tops were outfitted with burlap sacks. The maximum opening was 0.23 m2; however, the actual opening was often smaller because the cages were often deformed by cattle impact. Thus the opening size was measured at each collection. Litter is defined as leaves, seeds, and twigs $\leq$1 cm in diameter. The cages were maintained year-round and litter was collected three times per year with the last collection timed soon after maximum leaf fall.

Shrub biomass estimates for the interior 5-m radius of each NPP plot were based on light interception methods (sensu Reich and others 2001). A calibration curve relating shrub biomass to shrub leaf area index (LAI) was developed by harvesting all the biomass in the shrub layer (0.5 m to 2.5 m in height) in nine plots adjacent to the experimental watersheds. Before harvest, we measured shrub LAI using the techniques described above. We found a strong correlation between the two parameters (shrub mass in Mg ha^{-1} = 17.53 × shrub LAI, $r^2 = 0.95$, $p < 0.0001$).

Herbaceous layer aboveground net primary productivity (ANPP) was estimated by harvesting and weighing all herbaceous material from 0.0625 m^2 quadrats from within three randomly located, 1 m^2 livestock exclusion cages at peak standing crop (May 15 to June 15). Exclusion cages were randomly relocated each year post-harvest to avoid resampling or potential cumulative cage effects.

Fine root NPP (roots $\leq$ 2 mm diameter) was estimated using sequential coring (Vogt and others 1998, Fahey and others 1999). This method consists of estimating fine root production as the difference between live root biomass at minimum and maximum periods of plant growth. The method is most useful in systems that undergo distinct growth pulses such as annual grasslands (Fahey and others 1999). Hence, we collected three randomly located cores (15 cm depth, 5 cm inside diameter, AMS Core Sampler, American Falls, ID, USA) during the winter slow growth phase (December) for minimum and at peak standing crop (May/June) for maximum fine root biomass estimation. Soil cores were stored at 5ºC until being washed over a 1-mm mesh screen, which allowed us to collect all root and organic matter fragments trapped by the screen.

We used a variant of the stand increment approach (sensu Clark and others 2001) to estimate wood biomass and production. First, we developed allometric equations to predict aboveground woody biomass as a function of dbh. We combined the results from two separate studies of blue oak trees at SFREC (Millikin and others 1997, Dahlgren and Singer 1994) to obtain dbh and biomass estimates on eight trees (dbh range: 7.6 – 48.5 cm). For coarse root biomass (roots > 2 mm in diameter), we used the data from six trees in Millikin and others (1997). We applied the same allometric equations to calculate interior live oak biomass. There are no specific allometric equations for foothill pine, so we used the general equations that predict the aboveground woody biomass of pines from dbh (Jenkins and others 2003, *table* 3, species id = 100) and the equation from Omdal and others (2001) for Pinus ponderosa to estimate large-root biomass from dbh.

As noted above, we inventoried all the live trees (dbh ≥ 5 cm) in our plots in 2001. We censused these plots again in late September 2002 to document tree mortality and ingrowth. We also recorded the annual (October 2001 to September 2002) diameter growth from the subset of trees with dendrometer bands.

Statistical Framework

We evaluated the importance of differences in productivity among ecosystem components and watersheds by comparing means and their respective 95 percent confidence intervals. We explored the correlation of plot-level NPP with a suite of potential indicators, including tree basal area, canopy closure, herbaceous productivity, height of the herbaceous canopy, species richness, elevation, slope, and aspect. To visualize changes in tree, herb, and total NPP across the vegetation mosaic in the blue oak savanna, we smoothed the plot-level responses using locally weighted regressions (Cleveland and Devlin 1988). We used percent tree canopy closure (determined by light interception techniques; sensu Reich and others 2001) as the independent variable measuring proportional tree dominance.

Results

Productivity and Biomass

Annual estimates of mean NPP for the three experimental watersheds during 2001 to 2002 ranged from 4.35 to 5.69 Mg ha^{-1} yr^{-1} of dry biomass (*table* 1). Confidence intervals (95 percent) around these means averaged ± 33 percent of the mean. Given this variation, there were no significant differences in NPP between watersheds. Belowground production accounted for a low 18 percent of the NPP in WS1 and a high of 27 percent in WS2 (*table* 1). In general, there was much greater uncertainty in the belowground estimates.

Trees accounted for approximately 50 percent of ANPP in all three watersheds. In contrast, herb contributions were more varied. They produced 47 percent of ANPP in WS1, 39 percent in WS2, and only 35 percent in WS3 (*table* 1).

Live tree biomass was greatest in WS2 at 129 Mg ha^{-1} (*table* 2) with smaller pools in both WS1 (113 Mg ha^{-1}) and WS2 (111 Mg ha^{-1}). However, like NPP, these differences were not significant. Shoot-to-root ratios in live tree mass ranged from a low of 2.5 in WS1 to 3.3 in both WS2 and WS3 (*table* 2). Shrub mass was a consistently small component (1.4 -2.0 Mg ha^{-1}) of the live biomass pool in these watersheds, but they fixed proportionally more biomass (9 to 13 percent of ANPP, *table 1*).

Table 1—*Results from the Lewis Watersheds at Sierra Foothill Research and Extension Center, Browns Valley, CA. Fluxes reported in Mg ha^{-1} yr^{-1} of oven-dried biomass. x_r refers to the mean of 1000 randomizations of the estimated watershed value using stratified random sampling.*

Component	**WS1**		**WS2**		**WS3**	
(Mg ha^{-1} yr^{-1})	$\bar{x}_r$	95%CI	$\bar{x}_r$	95%CI	$\bar{x}_r$	95%CI
Herbs	1.91	1.59 – 2.26	1.61	1.23 – 2.07	1.20	0.80 – 1.72
Shrubs	0.39	0.24 – 0.52	0.43	0.25 – 0.59	0.45	33 – 0.57
Bole wood	0.88	0.71 – 1.04	1.15	0.81 – 1.54	0.92	76 – 1.10
Tree litter	1.41	1.03 – 1.81	0.97	0.71 – 1.25	0.89	0.66 – 1.12
ANPP	**4.59**	**3.97 – 5.28**	**4.13**	**3.51 – 4.80**	**3.47**	**2.87 – 4.06**
Fine roots	0.80	0.20 – 1.36	1.27	0.71 – 1.81	0.65	-0.01 – 1.32
Coarse roots	0.25	0.19 – 0.30	0.30	0.19 – 0.41	0.20	0.16 – 0.23
BNPP	**1.05**	**0.37 – 1.63**	**1.55**	**0.96 – 2.10**	**0.88**	**0.25 – 1.56**
NPP	**5.63**	**4.73 – 6.52**	**5.69**	**4.69 – 6.67**	**4.35**	**3.74 – 5.09**

Table 2—*Results from the Lewis Watersheds at Sierra Foothill Research and Extension Center, Browns Valley, CA. Pools reported in Mg ha^{-1} of oven-dried biomass. x_r refers to the mean of 1,000 randomizations of the estimated watershed value using stratified random sampling. CWD = coarse woody debris.*

Component	**WS1**		**WS2**		**WS3**	
(Mg ha^{-1})	$\bar{x}_r$	95%CI	$\bar{x}_r$	95%CI	$\bar{x}_r$	95%CI
Live mass						
Bole mass	82	70 – 96	99	76 – 122	85	69 – 102
Root mass	31	25 – 37	30	24 - 36	26	21 – 31
Shrub mass	1.4	0.72 – 2.0	1.7	1.0 – 2.4	2.0	1.4 – 2.6
Dead mass						
CWD	3.5	0.78 – 6.3	2.8	0.99 – 4.4	1.9	0.66 – 3.2
Dead trees	14	-12 – 38	0.60	-19 – 20	9.2	-14 – 35

There were important differences in the tree composition among the watersheds (*table* 3). The mean tree basal area was 14.7 Mg ha^{-1} (95 percent CI: 12.8 to 16.7), but tree basal area was notably but not significantly lower on WS3 (11.7 m^2 ha^{-1}) compared to the other two watersheds (*table* 3). The pine fraction was much higher in WS2 (20 percent of basal area), whereas interior live oak was more abundant in WS3 (28 percent of basal area). Paralleling the differences in the tree stratum, understory plant composition varied among the watersheds (Multiple Response Permutation Procedure, p < 0.001, McCune and Grace 2002). For example, *Rhamnus californica* (coffeeberry) was more abundant and frequent in WS3, while *Bromus madritensis* (red brome), an introduced non-native annual grass, was a major component of the understory flora in WS1.

Table 3—Results based on 2001 inventory from the Lewis Watersheds at Sierra Foothill Research and Extension Center, Browns Valley, CA. Watershed-level means (standard error of the mean) of tree basal area and density calculated from a stratified random sample of 12 plots per watershed.

Species	**WS1**		**WS2**		**WS3**	
	density (%)	basal area (%)	density (%)	basal area (%)	density (%)	basal area (%)
Blue oak	95.2	89.9	56.7	52.4	60.1	58.6
Foothill pine	2.8	8.1	20.5	20.2	6.0	7.8
Interior live oak	1.9	1.9	19.2	19.2	33.0	28.1
Black oak[1]	0.2	0.1	3.6	8.1	--	--
Ponderosa pine[1]	--	--	--	--	1.0	5.5
Totals	stems ha^{-1}	m^2 ha^{-1}	stems ha^{-1}	m^2 ha^{-1}	stems ha^{-1}	m^2 ha^{-1}
	550 (241)	16.6 (2.3)	438 (75)	15.7 (1.9)	317 (36)	11.7 (0.6)

[1] Black oak (*Quercus kelloggii*) and ponderosa pine (*Pinus ponderosa*).

Patterns in Productivity

From the suite of potential indicators, tree basal area was the most strongly correlated with plot-level NPP (r = 0.63, p < 0.001. *fig.*1A). The next best was a positive relationship with herb productivity (r = 0.49, p = 0.003, *fig.* 1B). No other correlations with NPP had a coefficient better than ± 0.30.

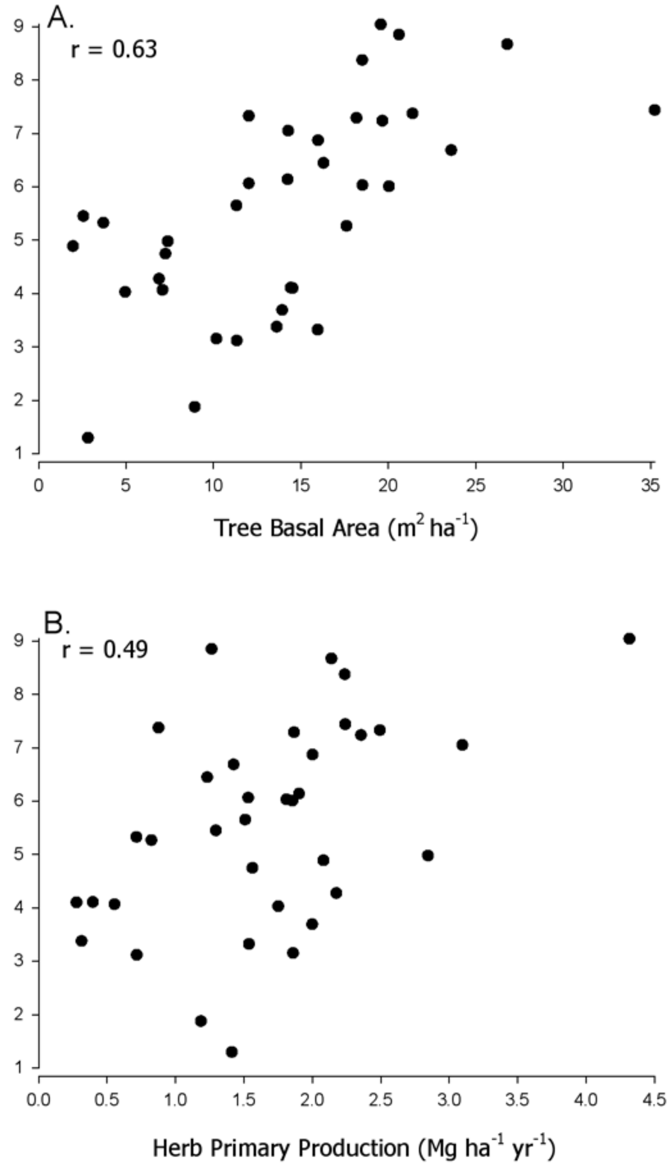

Figure 1—Correlation between plot-level estimates of total NPP and tree basal area (A) and herb productivity (B) in a Californian blue oak savanna.

Tree productivity increased in a linear fashion with canopy closure (*fig*. 2). In contrast, herb productivity was nearly constant for relatively open sites (canopy closure < 40 percent) and then monotonically declined as canopy closure increased. The result is that total NPP increased gradually from the most open sites in the watersheds to a maximum near 55 percent canopy closure. At higher canopy cover there was little change in total NPP (*fig*. 2) though the ratio of tree biomass to herb biomass continued to increase.

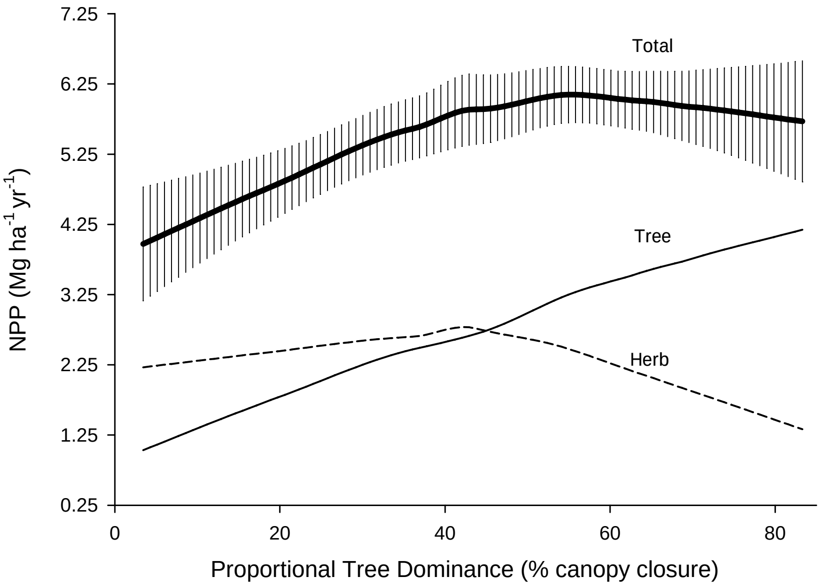

Figure 2—Regression models of productivity versus tree dominance in a Californian blue oak savanna. The final regressions were based on local linear models with the smoothing parameter set to 0.75 (Cleveland and Devlin 1988). Error bars for total NPP are the standard errors of the fit. The coefficient of variation (CV = standard error of the fit over the fit) for NPP = 10 percent; for tree productivity CV = 16 percent; for herb productivity, CV = 15 percent.

Discussion

Our watershed-level estimates of biomass and NPP for the blue oak savanna (*table* 1, *table* 2) fell within the wide range of values reported for this diverse biome. While the live biomass pool was near the global mean for tropical savannas, productivity was closer to the low end of the range (Chen and others 2003, House and Hall 2001). As a consequence, the biomass-to-NPP ratio for the blue oak savanna (23 years) was much higher than the global mean for savannas (3.4 years, Chen and others 2003). Clearly carbon in the blue oak savanna is cycled much more slowly than expected for a savanna ecosystem.

In general, the low productivity of the blue oak savanna is typical of more arid tropical sites that support tree-grass ecosystems. For temperate savannas, our ANPP results (table 1, watershed mean = 4.06 Mg ha-1 yr -1) closely matched two recent findings. Reich and others (2001) measured biomass and productivity in 20 oak savanna stands in eastern Minnesota. Extrapolating from the reported regression relationship, ANPP in comparable stands in Minnesota (i.e., stands with a canopy openness around 44 percent) was around 3.75 Mg ha-1 yr-1. Mitchell and others (1999) documented an ANPP gradient from a low of 3.91 Mg ha-1 yr-1 in xeric sites to a high of 7.43 Mg ha-1 yr-1 in mesic sites for pine-wiregrass ecosystems in Georgia.

The productivity of our research watersheds is broadly representative of the blue oak savanna in California. Long-term forage (i.e., herb productivity) records indicate that Sierra Foothill Research and Extension Center (SFREC) has yields comparable to other oak savannas in California (George and others 2001). In regard to temporal patterns, 2002 was an average year in terms of herb productivity. From monitoring sites across SFREC between 1980 and 1999, annual average productivity ranged from a minimum of 1.2 Mg ha^{-1} yr^{-1} to a maximum of 5.3 Mg ha^{-1} yr^{-1} (George and others 2001). However just as we have found (*fig*. 2), Connor and Willoughby (1997) showed that herb productivity in the blue oak savanna varies relative to canopy cover. The long-term average forage yield at SFREC for sites with 50 percent canopy cover (a canopy level close to the 56 percent mean canopy measured in our research watersheds) was 1.58 Mg ha^{-1} yr^{-1}, an estimate commensurate with the mean of our three watersheds (1.57 Mg ha^{-1} yr^{-1}).

Acorn production is a spatially and temporally variable element of the productivity budgets of blue oak savannas. For California oaks, annual acorn output varies greatly both interannually and geographically (Koenig and others 1996, Koenig and others 1999). At SFREC, Dahlgren and Singer (1994) reported an average acorn production under blue oak canopies of 2.69 Mg ha^{-1} yr^{-1} but during the three years of observation (1990 to 1992) yields varied from 0.3 to 5.8 Mg ha^{-1} yr^{-1}. In 2002, acorns made a negligible contribution to the NPP of our research watersheds but clearly acorn production is a major component of NPP. It will be interesting to examine the relationship between tree growth and reproductive output as our long-term record develops.

In 2002, watershed-level means of leaf litter production varied from 1.41 Mg ha^{-1} yr^{-1} in WS1 to 0.89 Mg ha^{-1} yr^{-1} in WS3 (*table* 1). These values fall toward the low end of the range reported for blue oak savanna (1.4 to 2.1 Mg ha^{-1} yr^{-1}, Dahlgren and Singer 1994, Knops and others 1996).

Root productivity is a notoriously difficult parameter to measure (Vogt and others 1998) and we acknowledge the limitations of our min-max approach by reporting the large uncertainties associated with the means (*table* 1). Our watershed-level estimate of 0.9 Mg ha^{-1} yr^{-1} of fine root production (*fig*.1) is half the production reported by Cheng and Bledsoe (2002). They calculated their estimate from sequential harvesting of ingrowth cores in a nearby blue oak watershed at SFREC. However, despite their physical proximity, direct comparisons between the studies are difficult. Ingrowth cores tend to overestimate root biomass (Steingrobe and others 2000). Moreover, the studies were done in different years and conducted at different spatial scales (topographic sites versus whole watersheds). Nevertheless, the range of our values from individual plots overlapped with the range of value reported in Cheng and Bledsoe 2002.

Living woody biomass dominated the carbon pool in these watersheds (*table* 2). Dead biomass (dead trees and coarse woody debris) accounted for a characteristically small portion of the budget. As Tietje and others (2002) documented, dead biomass does not accumulate in the blue oak savanna. Given the compositional dominance of the annual plants in the herb layer, it is reasonable to infer that dead herbaceous tissue made an even smaller contribution to the biomass pool. We did not measure soil organic matter in the research watersheds, but Dahlgren and others (2003) reported that soil organic matter (surface 15 cm) averages approximately 110 Mg ha^{-1} under oak canopies and 50 Mg ha^{-1} in open grasslands for comparable sites at SFREC.

Tree-Grass NPP Ratio

The empirical pattern we described for the relationship between NPP and the tree-grass ratio in the blue oak savanna (*fig*. 2) does not precisely match any of the conceptual models described in House and others (2003). Across these research watersheds, total NPP increased linearly with increasing canopy cover until it saturated at approximately 50 percent cover. Herb productivity did not decline until this saturation point was reached. In contrast, tree NPP increased monotonically with canopy cover across the observed range. Thus, it appears that the interaction between the trees and grasses is contingent upon where they are on the landscape. In the more open areas, tree and grass productivity do not seem to be related, as predicted by McClaran and Bartolome (1989). However, as the proportional dominance of trees increased beyond ~50 percent canopy cover, grass productivity was negatively impacted. These results generally correspond to the findings of Connor and Willoughby (1997) that canopy cover levels of 40 percent to 60 percent do not suppress forage production in the blue oak savanna.

The factors that determine the abundance of trees and grasses in savannas continue to be debated (Sankaran and others 2004). Resolution of this debate will require a comprehensive approach to savanna ecology. Our results concerning the productivity of this Mediterranean savanna explicitly incorporated the spatial complexity of these ecosystems. We contend that the uncertainty associated with these NPP estimates provide a crucial and underappreciated dimension to our understanding of this ecosystem. Future work will address the temporal variability in tree-grass productivity relationships and the impact of land-use changes. Given the documented sensitivity of savannas to changes in land use (House and others 2003), we need methods to evaluate the impact of these changes on ecosystem function at relevant spatial scales. The biometric approach described here provides an initial estimate of the resolution of any changes in NPP that we can expect to detect in a small watershed.

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Continue

Solving a Mediterranean Mystery: Why Do Winter-Deciduous Trees Dominate Some Woodlands?[1]

Chris Ineich[2]

Abstract

Current theory suggests Mediterranean climates favor evergreen over winter-deciduous vegetation because the former can sustain photosynthetic production during the mild winter when water is not limiting. However, winter-deciduous trees, especially oaks, are not uncommon in some Mediterranean regions, and frequently replace evergreens in the most xeric upland savannas as well as in very mesic riparian forests. To explain this anomalous distribution of deciduous dominance, I have developed a simple mechanistic model of leaf habit for Mediterranean climates. The model is based on the relative photosynthetic C economy of evergreen vs. winter-deciduous leaves during two developmental stages, and predicts a bimodal distribution of deciduous-dominance along a moisture gradient. The higher intrinsic photosynthetic capacity of deciduous relative to evergreen leaves should allow drought-adapted deciduous species to grow roots more rapidly over the first wet season, and thereby recruit in environments too xeric to support otherwise similar evergreens. Where moisture is sufficient for seedlings of both habits to establish, the advantage should go to the strategy that maximizes photosynthetic C gain, and thus growth, over a year. If the summer drought period is very short (e.g. riparian forests), winter-deciduous leaves achieve the larger annual C gain because they can extend their intrinsic photosynthetic advantage over a longer season each year. Where the drought period becomes sufficiently long, however, evergreen leaves gain the advantage because they can continue photosynthetic production through winter when deciduous species are inactive, and thereby more than compensate for their lower spring-time assimilation rates. I am currently testing the predictions of this model for several evergreen and winter-deciduous California oaks. I will briefly discuss these projects as well as the management implications of this work.

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[1] An abbreviated version of the paper was presented at the Sixth California Oak Symposium: Today's Challenges, Tomorrow's Opportunities, October 9-12, 2006, Rohnert Park, California.

[2] University of California, Davis. e-mail: cdineich@ucdavis.edu.

Continue

Disturbance

Continue

Effects of Mule Deer and Bison on Regeneration of Island Scrub Oak on Santa Catalina Island, California[1]

Thad A. Manuwal[2] and Rick A. Sweitzer[2]

Abstract

Islands commonly harbor unique species that are particularly susceptible to damage by introduced organisms. Historically, no large ungulates existed on Santa Catalina Island, but several were introduced, including mule deer (*Odocoileus hemionus*) and bison (*Bos bison*). A recently completed study suggested bison may alter the structure of island scrub oak (*Quercus pacifica*) woodlands but no data exists for assessing impacts of mule deer to endemic trees and shrubs on the island. We are investigating this and other aspects of deer ecology on Santa Catalina Island during a study from January 2005 to August 2007. Our research was designed to estimate habitat use and diets, measure browse use of trees and shrubs, characterize current regeneration of scrub oak woodlands, and identify factors impinging on oak seedling survival, using data from multiple plots in which 1,600 total seedlings were planted in 2005. This report focuses on scrub oak woodland regeneration and seedling mortality. Our results suggest scrub oak seedling numbers are recovering in some areas of the island, likely related to recent removal of feral pigs and feral goats. Relatively large seedlings remain uncommon, potentially due to browsing by abundant mule deer. Nevertheless, physical damage to seedlings by bison appears more important for reduced seedling survival than browsing by mule deer.

Keywords: Bison, California, feral pigs, feral goats, Quercus pacifica*, regeneration*

Introduction

The introduction and spread of nonnative species is an important conservation problem in general but especially on islands (Cree and others 1995, Savidge 1987), which typically have higher proportions of endemic species than mainland ecosystems and are more prone to invasion (Lodge 1993, Simberloff 1994). Large ungulates introduced to islands can be highly irruptive (Andersen and Linnell 2000) where they may cause important browse damage to endemic trees and shrubs that lack adequate chemical and structural defenses (Bowen and Van Vuren 1997, Husheer and others 2003).

Santa Catalina Island (hereafter Catalina Island), part of California's Channel Islands (a small group of islands off the coast of Southern California), has a long history of introduced ungulates, including mule deer (*Odocoileus hemionus*). Catalina Island was occupied by feral goats (*Capra hircus*) before mule deer were introduced in the early 1930s (Coblentz 1977), whereas bison (*Bos bison*) and feral pigs (*Sus scrofa*) were introduced around the same time as mule deer (Sweitzer and others 2005). By the 1980s, conservationists were more aware of the myriad ecological problems with introduced species. In the 1990s, the Santa Catalina Island

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[1] An abbreviated version of this paper was presented at the Sixth California Oak Symposium: Today's Challenges, Tomorrow's Opportunities, October 9-12, 2006, Rohnert Park, California.

[2] Graduate student and Associate Professor, respectively, Department of Biology, University of North Dakota, Grand Forks, ND 58202. e-mail: thad.manuwal@und.nodak.edu; richard_sweitzer@und.nodak.edu.

Conservancy (hereafter Conservancy), a non-profit organization that owns and manages 88 percent of Catalina Island, implemented an active restoration program to eradicate feral goats and feral pigs (Schuyler and others 2002). By early 2005, feral goats were eradicated and nearly all feral pigs had been removed (Schuyler and others 2002, Conservancy records). Recently completed research on the bison population provided useful information on their ecological effects (Constible and others 2005, Sweitzer and others 2003), thereby supporting a controversial decision by the Conservancy to reduce but not entirely remove the bison herd. Mule deer remain widespread and abundant at an unknown level, however, and very little is known of their foraging behaviors and population ecology useful for management.

Catalina Island contains 6 island endemic and 15 Channel Islands endemic plant species that may be in danger from impacts of introduced ungulates. Recent observations of island scrub oak (*Quercus pacifica*), a Channel Islands endemic, have indicated low regeneration rates and browse damage caused by mule deer. Due to the ecological importance of oak species (Pavlik and others 1995) we designed a study to investigate the impacts of introduced ungulates on oak seedling recruitment. Specifically, our objectives in this study were to use seedling belt transects to characterize the current regeneration potential of island scrub oak woodlands, and experimentally assess factors contributing to island scrub oak seedling mortality. We hypothesize that mule deer browsing is limiting regeneration of island scrub oak and browsing activities will be an important factor of island scrub oak seedling mortality. In addition, various environmental factors (vegetative height and protective cover) should positively influence seedling survival by protecting the seedling from ungulate disturbance.

Methods

Study Area

Catalina Island is a 194-km^2 island located 40 km south of coastal Los Angeles, in Los Angeles County. Elevation on the island ranges from sea level to 640 m, with a topography dominated by a northwest-southeast mountain range containing a series of lateral canyons (Schuyler and others 2002). The climate is Mediterranean with relatively mild temperatures throughout the year and a long-term mean annual precipitation of 290 mm, mostly occurring between November and April (Schoenherr and others 1999). There are four common habitat types on the island: (1) coastal sage scrub, characterized by coastal sage (*Artemisia californica*) and prickly pear cactus (*Opuntia littoralis*); (2) grassland, dominated by exotic annual grasses and forbs, such as wild oats (*Avena fatua*) and storksbill (*Erodium* spp.), interspersed with native bunch grasses (*Nasella* spp.); (3) island chaparral, represented by evergreen and drought-resistant shrubs and low trees such as island scrub oak and lemonade berry (*Rhus integrifolia*); and (4) riparian habitats limited to a few permanent or ephemeral streams in relatively deep canyons and marshy wetland areas that are represented by cottonwood (*Populus trichocarpa*), willow (*Salix* spp.) various sedges and rushes, and mule fat (*Baccharis pilularis*) (Knapp 2002).

Three cross-island fences were established on Catalina Island in the 1990s to facilitate the eradication of feral pigs and goats (Schuyler and others 2002), effectively dividing the island into four zones (*fig.* 1). These two feral ungulates were then eradicated in each zone sequentially (zone one– 1998, zone two – 2000, zone three – 2003, zone four – all goats and most pigs by January 2005). Because feral pigs are known to negatively impact tree seedling survival by rooting (Sweitzer and Van Vuren 2002) and feral goats seriously damage trees and shrubs by browsing (Coblentz 1977), we anticipated potential differences among zones one, two, and three for the number and size of scrub oak seedlings. Further, because bison on Catalina Island rarely ventured across the isthmus into zone one historically, and were prevented from crossing into zone one by fence after the early 1990s (Sweitzer and others 2005), any possible bison-related impacts to tree seedlings would be focused in zones two and three.

Scrub Oak Regeneration

Feral ungulates may impact tree seedling survival in general and scrub oak regeneration on Catalina Island in particular by rooting (feral pigs), browsing (mule deer, feral goats), and trampling or wallowing (bison). Tree seedling "belt transects" can be used to assess the impacts of foraging ungulates on seedling survival and forest regeneration (Bruinderink and Hazebroek 1996, Sweitzer and Van Vuren 2002), and we therefore enumerated and measured sizes of naturally growing tree seedlings along multiple 4-m X 40-m belt transects in three different "zones" on Catalina Island, demarcated by cross-island fences. To begin to understand the potential impacts of mule deer and feral pigs and goats on tree seedling survival, we used the Santa Catalina Island geographic information system (GIS) to randomly identify starting positions for 5, 12, and 13 seedling belt transects in large blocks of scrub oak woodlands in zone one, zone two, and zone three, respectively. Fewer transects were done in zone one because the overall area of scrub oak woodland is

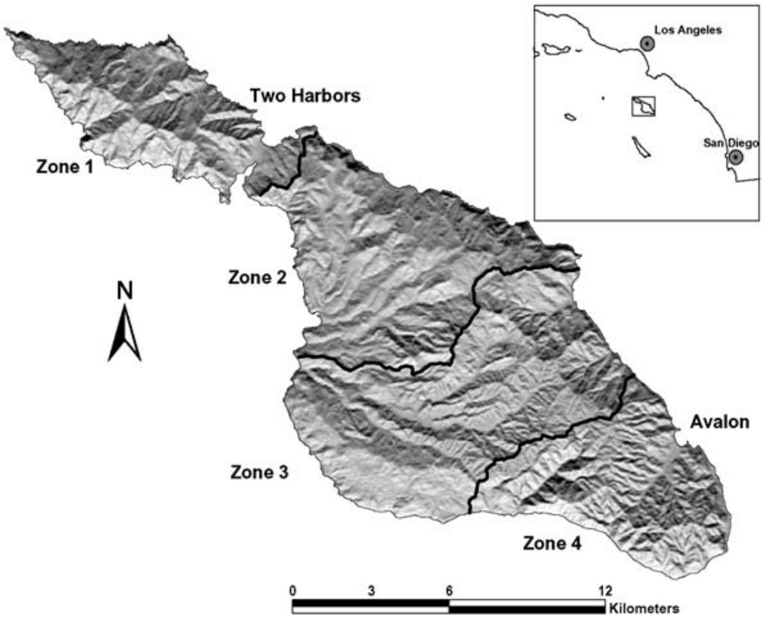

Figure 1—Map of Catalina Island illustrating locations of three cross-island fences, established in the 1990s, which partitioned the island into four feral animal removal zones. Inset in the upper right shows the location of Catalina Island in relation to mainland southern California and several nearby Channel Islands.

less in this region of Catalina Island than in zones two and three (2839, 5192, and 6509 ha in zone one, two, and three; respectively).

Belt transects were assessed during July and August 2005. From starting positions for each belt transect, we randomly selected an azimuth from 0 to 359° N and laid out a 40-m line transect. All tree seedlings encountered within 2 m 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.

A one-way Analysis of Variance (ANOVA) was used to compare the mean number of oak seedlings among the three zones (data on mean seedling number/transect were transformed by natural log prior to analysis; Zar 1999). In a second analysis of data from seedling transects, we calculated an index to regeneration potential as the ratio of large scrub oak seedlings (>200 mm) to total scrub oak seedlings for each belt transect (Sweitzer and Van Vuren 2002). A low regeneration index suggests that relatively few tree seedlings survived to a relatively large size in which they may be less prone to current and future mortality caused by mule deer or bison activity. Regeneration index data were arcsine transformed to meet assumptions of normality and evaluated by ANOVA.

Oak Seedling Mortality Factors

From January to March 2005, we planted 1,600 (1- to 3-year-old) greenhouse-grown island scrub oak seedlings in sixteen 30-m by 30-m experimental seedling plots in island scrub oak chaparral habitats (100 oak seedlings/plot). Prior to out-planting, all seedlings were measured for total height and ranked by health status. Data on seedling sizes were compiled and used to partition seedlings into four different size classes (size class one <100mm, size class two- 101 to 200mm, size class three- 201 to 300mm, size class four >300mm). The distribution of tree seedlings among the size classes constrained our design such that each seedling plot could include 33 seedlings within size class one, 34 seedlings within size class two, 20 seedlings within size class three, and 13 seedlings within size class four. We used a randomization procedure to identify and select 100 individual seedlings among the four size classes for each of the 16 different experimental seedling plots.

The Santa Catalina Island Conservancy’s GIS database was used to identify seedling plot locations, based on the goal of planting a minimum of three seedling plots within each of the five focus areas (we planted an extra plot in the Twin Rocks focus area, *fig. 2*). A 100-m by 100-m grid was placed over island scrub oak habitats that fell within a 400-m buffer strip around drivable roads on the island (*fig. 2*), rendering plot locations reasonably accessible for hand-carrying seedlings and planting equipment to the area. We utilized a randomization method to select grid cells for planting; the first three random grids in each focus area that encompassed a 30-m by 30-m area suitable for planting were used for seedling plots. Grid areas were considered unsuitable for planting when soils were very rocky, overly steep, or not scrub oak woodland.

Each 30-m by 30-m seedling plot (hereafter seedling plot) was subdivided into 100 3-m by 3-m cells for planting. Individual tree seedlings were planted in the approximate center of each plot cell unless trees, rocks or other obstacles prevented planting access to that area of the cell with a two person gas-powered soil auger. The soil auger was fitted with a 20-cm diameter bit for excavating a 40- to 45-cm planting hole. Augered planting holes were cleared of loose soil whereupon seedlings were carefully extracted from their nursery tubes with root balls intact and placed into the hole with stems at approximate ground level. Excavated soil was used to backfill around each seedling and tamped firmly into place using a hand trowel.

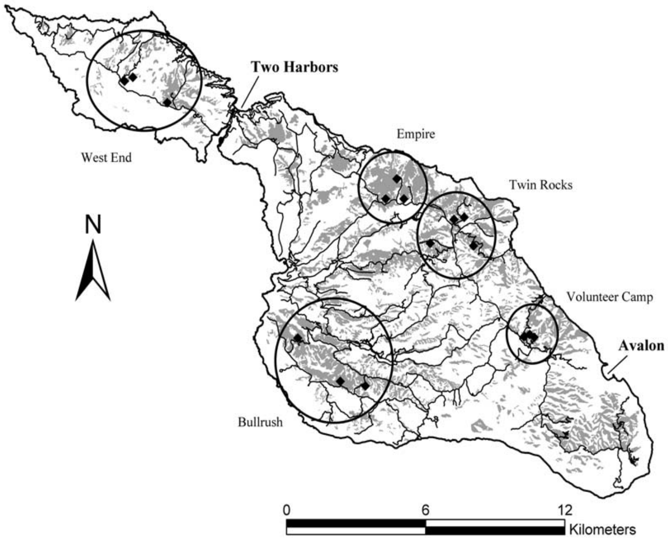

Figure 2—Locations of sixteen experimental seedling plots (black diamonds) established in five study areas (black ovals) of Catalina Island, California. Shaded areas represent island scrub oak woodland habitats.

Seedlings at two seedling plots were “watered in” with 7.5-9.5 l of water per seedling slowly drained into the soil from plastic water containers placed on the edges of the refilled holes. Watering in was not done at the other 14 seedling plots because soils were very moist from winter rains that occurred before and during the planting period.

We visited and evaluated all seedling plots approximately every six weeks from March to August in 2005, and from January to July in 2006, for a total of eight monitoring periods. During each plot visit and for each individual seedling, we recorded data on seedling status (alive/dead), general health (poor, good, or very good), seedling height (tallest apical bud standing in a natural position ± 2 mm), evidence of deer browse of seedlings (any branchlets that were browsed were hand clipped perpendicular to axial growth to preclude recounting on subsequent visits), direct (hoof print on seedling, bison wallow) and indirect ungulate activity within 1-m radius of each seedling, surrounding cover type (beneath tree canopy, open, within cover such as woody debris or prickly pear cactus), and vegetative cover (height of herbaceous vegetation immediately surrounding the seedling).

We used a logistic regression model to investigate factors contributing to survival and/or mortality of island scrub oak seedlings in the seedling plots. Predictor variables included in the model were browse disturbance [BR_DIST (expressed as the number of times an individual seedling was browsed/the number of times that seedling was recorded as alive)], ungulate disturbance [UNG_DIST (total number of times an individual seedling was disturbed by ungulate activity with the exception of browse/ total number of times seedling was alive)], other disturbances [OTHER_DIST (number of times an individual seedling was disturbed by rodents, insects or other/ number of times seedling was alive)], indirect disturbances [IND_DIST(number of times ungulate activity was observed within 1-m radius of seedling/ total number of times seedling was alive)], cover [COVER (whether or not seedling was positioned in protective cover or not)], canopy position [CNPY (whether or not seedling was positioned under canopy or not)], and vegetative cover [VEG_COV (expressed as the mean of vegetation height minus seedling height over all monitoring periods)]. All predictor variables that were ratios were transformed using the arcsine transformation prior to analyses (Zar 1999). A backward selection method was used to reduce the model, in which the least significant terms (highest P-values) were removed sequentially until all terms remaining in the model were significant ($\alpha < 0.05$). Logistic regression analyses were performed using statistical software R (R Development Core Team 2005).

Results

Scrub Oak Regeneration

Scrub oak seedlings were significantly more numerous for belt transects conducted in zone one of Catalina Island compared to zones two and three (*table* 1; $F_{2,26} = 4.24$, $P = 0.025$). Based on analyses of the ratios of large seedlings to total seedlings, however, there were proportionally similar numbers of large seedlings among the three zones (*fig*. 3; $F_{2,26} = 1.08$, $P = 0.35$).

Oak Seedling Mortality Factors

Seventy-six percent of the 1,600 island scrub oak seedlings we planted in the experimental seedling plots remained alive as of July 2006, and most (70 percent) are in good to excellent condition. On average, 4.9% ± SE 0.57 of the 1,600 planted seedlings experienced some type of disturbance between monitoring periods. Deer browsing was by far the most common type of disturbance observed; an average of 3.7% ± SE 0.3 of the 1,600 planted seedlings had evidence of browsing during each monitoring period (*fig*. 4). In general, the large majority of disturbance to planted oak seedlings was by nonnative ungulates (*fig*. 4).

Table 1—*Summary data for island scrub oak seedlings detected along seedling belt transects for different areas of Catalina Island, California. Data are from July and August 2005.*

Zone	Number transects	Total area sampled (m^2)	Total oak seedlings	Mean number oak seedlings (SE)	Seedling density (seedlings/m^2)
1	5	800	2312	462 (217.1)	2.89
2	11	1760	458	42 (21.3)	0.26
3	13	2080	665	51 (20.3)	0.32

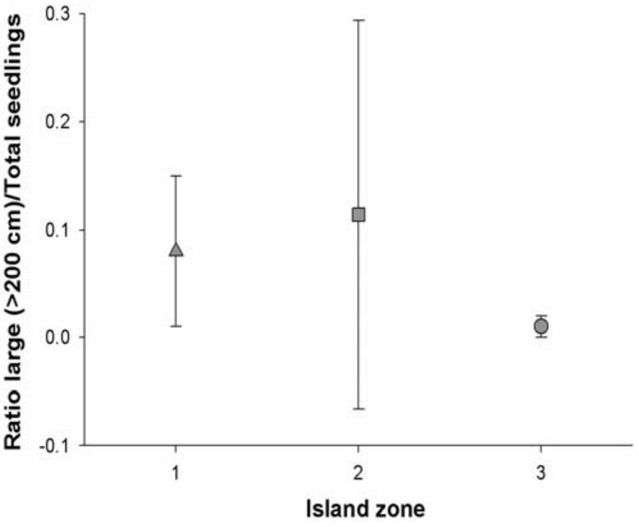

Figure 3—Comparison of mean regeneration ratios (± 1 SE) for island scrub oak seedlings based on seedling belt transects in different areas of Catalina Island in 2005.

Logistic regression analyses of data on scrub oak seedlings after eight monitoring visits (17 to 18 months after seedlings were planted) identified ungulate disturbance, protective cover, overhead canopy, and vegetative cover as important predictors of survival (*table* 3). Our final reduced model was:

$$g(x) = 2.25 - 0.87(UNG\_DIST) - 1.48(IND\_DIST) - 0.006(VEG\_COV)$$

Seedlings that experienced ungulate disturbance were located in areas with repeated ungulate activity, and those within herbaceous vegetation taller than the seedling were less likely to survive than seedlings experiencing no ungulate disturbance, those that were not in areas of ungulate use, and those that were taller than the surrounding herbaceous layer (*table* 3). Seedlings that had some evidence of browsing by mule deer did not experience lower probabilities of survival than non-browsed seedlings (*table* 2).

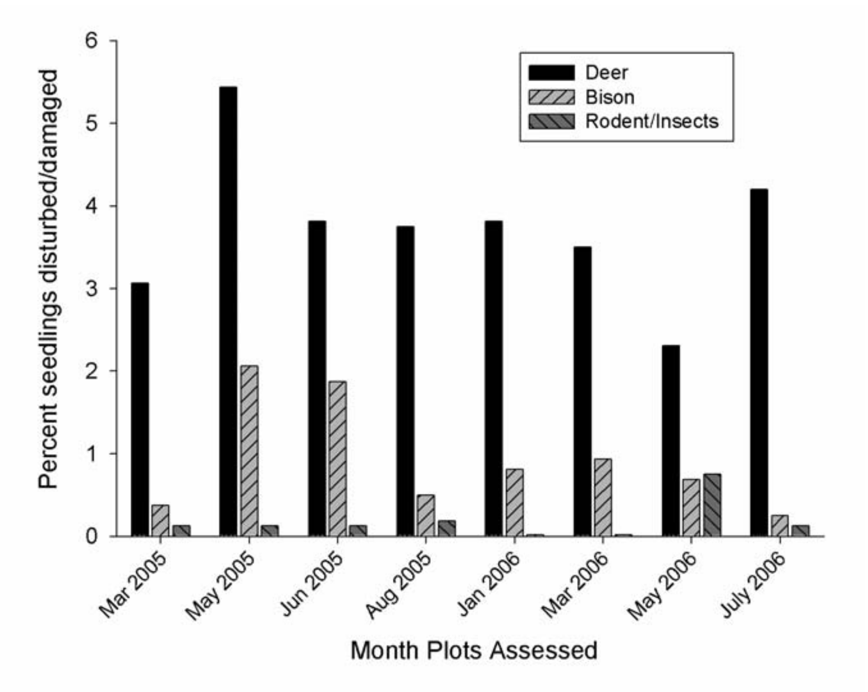

Figure 4—Identified sources of disturbance (browsing, trampling, chewing, etc.) for scrub oak seedlings planted among 16 experimental seedling plots on Catalina Island, California.

Table 2—*Summary of coefficient estimates and their associated statistics for the full logistic regression model with response variable - oak seedling survival. See Methods for description of variables.*

Variable	Coefficient	S.E.	z statistic	p-value
CONSTANT	2.267	0.160	14.187	< 0.0001
BR_DIST	0.501	0.365	1.375	0.1692
UNG_DIST	-0.810	0.382	-2.117	0.0343
OTHER_DIST	-0.791	1.085	-0.730	0.4655
IND_DIST	-1.438	0.217	-6.626	< 0.0001
COVER	0.365	0.237	1.540	0.1236
CNPY	-0.198	0.141	-1.408	0.1593
VEG_COV	-0.005	0.001	-8.621	< 0.0001

Table 3—*Summary of coefficient estimates and their associated statistics for the reduced logistic regression model with response variable - oak seedling survival. See Methods for description of variables.*

Variable	Coefficient	S.E.	z statistic	p-value
CONSTANT	2.246	0.115	19.605	< 0.0001
UNG_DIST	-0.874	0.382	-2.288	0.0222
IND_DIST	-1.477	0.214	-6.899	< 0.0001
VEG_COV	-0.006	0.001	-9.170	< 0.0001

Discussion

Data from seedling belt transects suggest important variation in numbers of oak seedlings growing in different areas of Catalina Island. Oak seedlings appeared over 10 times as abundant on the west end of the island (zone one, *fig 1*) compared to two regions encompassing the central portion of the island (*table* 1, *fig 1*). Feral pigs and feral goats were eradicated from the zone one area of Catalina Island nearly four years and more than six years before these ungulates were eradicated from zone two and zone three, respectively (Schuyler and others 2002). Bison have also been excluded from zone one historically. Together these preliminary findings suggest seedling numbers are recovering in zone one by release from rooting and other activities of feral pigs and goats. The large number of seedlings found in zone one may also reflect the absence of bison trampling activities in this area. Even though seedlings were more abundant in zone one, there was no difference in the number of large seedlings relative to total seedlings in this area compared to zones two and three (*fig. 3*). It is possible that the persistent lack of large seedlings in the western region of Catalina Island and in zones two and three is because of ongoing browsing by mule deer, which are abundant in all three zones of the island.

Mean regeneration ratios in zone two exhibited a high level of variability compared to regeneration ratios in zones one and three. Although we are currently unable to offer an explanation for this pattern based on the activities of mule deer, bison, or recently eradicated feral pigs and goats, we anticipate that an additional series of seedling transects will aid in verifying that the pattern was not an artifact of sampling effort.

Direct and indirect disturbance to tree seedlings in the form of trampling and bison wallowing were more important predictors of island scrub oak seedling mortality than browsing by mule deer. Several studies have addressed physical disturbances to oak seedlings (Sweitzer and Van Vuren 2002) but few have specifically addressed trampling activities by large ungulates. Similar to our results, Coppedge and Shaw (1997) found that bison on the Tallgrass Prairie Preserve in Oklahoma significantly impacted saplings and shrubs by horning and rubbing activities. They further concluded that bison activity could have effectively limited the historic distribution of woody vegetation in the Great Plains. Although our seedlings were too small for rubbing or horning, the above studies support our findings that disturbances by large ungulates can limit recruitment of trees and shrubs.

When designing the study, we originally anticipated that vegetative cover would obscure seedlings from foraging mule deer, thus positively influencing seedling survival. However, the logistic regression model identified relatively tall vegetative cover as a negative influence on seedling survival. These results are in accordance with observations in the field that a large proportion of seedlings growing in areas dominated by tall and dense non-native grasses appeared less vigorous. Although our study does not address the mechanisms by which this process occurs, it is possible that herbaceous vegetation [mostly non-native grasses (*Avena* spp., *Brachypodium distachyon*, *Bromus* spp.) in our study plots] reduces water, soil nutrients, and light availability for the relatively small scrub oak seedlings. Interactions between oak seedlings and exotic annual grasses were identified as limiting factors to seedling survival in other studies. Danielsen and Halvorson (1991) found that valley oak (*Quercus lobata*) seedling growth and survivorship were limited by exotic annual grasses, and Gordon and Rice (2000) determined the importance of soil water potential competition between blue oak (Q*uercus douglasii*) seedlings and exotic grasses. Our results suggest that island scrub oak seedlings may experience similar detrimental effects from nonnative grass species.

Oak seedling survival can vary significantly with differences in annual precipitation, with low seedling survival in drought years and high seedling survival in wet years. Catalina Island's annual precipitation for calendar year 2005 was 527.05 ± SE 23.84 mm, the second highest in recorded history. This is approximately 200 mm above long-term average precipitation and likely contributed to the high survival of our planted seedlings. During periods of drought or more normal rainfall conditions, seedling survival could be reduced from the 76 percent we report 1.5 years after planting. In addition, the wet conditions likely increased the amount of available forage for mule deer, potentially decreasing browsing pressure on seedlings. Browsing pressure from deer could become a more significant mortality factor for island scrub oak seedlings in years with limited available forage. Continued monitoring of these plots will allow a more comprehensive look at inter-annual precipitation effects on island scrub oak seedling mortality.

The results we have presented from this study are important for identifying the effects of introduced ungulates on scrub oak woodland habitats on Catalina Island. The recent removal of feral pigs and feral goats may be contributing to establishment of many oak seedlings on one part of the island (zone one), but relatively large seedlings that may eventually recruit to canopy forming trees and thereby contribute to the maintenance of scrub oak woodland habitat appear limited in number island-wide. Although browsing by mule deer does not appear to kill scrub oak seedlings outright, it may prevent free-growing seedlings from becoming saplings of sufficient size/height to escape herbivory by mule deer. Further, data from our experimental seedling plots have revealed that trampling and wallowing by bison may be at least partly responsible for the relatively low numbers of oak seedlings detected along seedling belt transects in zones two and three compared to zone one. Recall that bison have not historically ranged into the zone one area of Catalina Island during their 80-plus year history on the island.

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Continue

Distribution of Nonnative Red Foxes in East Bay Oak Woodlands[1]

Allison L. Bidlack,[2] Adina Merenlender,[2] and Wayne M. Getz[2]

Abstract

European red foxes (*Vulpes vulpes*) were introduced into lowland California in the 1880s for fur farming and hunting. The introduced foxes quickly spread throughout much of the state and have been implicated in the decline of several federally threatened and endangered ground-nesting bird species. Red foxes have been present in the East Bay for 25 to 30 years and they are regularly sighted in coastal wetlands and in the Oakland and Berkeley hills. We were interested in documenting the extent of the invasion away from human-dominated habitats into oak woodlands in the East Bay, as foxes may negatively impact both prey populations and native carnivores such as gray foxes. We surveyed fire roads and hiking trails in core oak woodland sites in Contra Costa and Alameda counties for carnivore scat. All scat samples were collected, and their locations entered into a GIS. To positively distinguish the scat to species, DNA was extracted, amplified, and identified using Polymerase Chain Reaction (PCR) and Restriction Fragment Length Polymorphism (RFLP) testing. Four carnivore species were identified, including coyote, gray fox, red fox, and bobcat. Red foxes were only detected in woodlands that were adjacent to urban or suburban development, and were not detected in more rural sites. They may be dependent on human-dominated systems for resources and cover, and the high numbers of coyotes present in the East Bay may be excluding them from some areas. This research is providing managers essential information about red fox distribution, habitat requirements, and interactions with other carnivores, which can be used to better monitor and eventually control red fox invasions and subsequent impacts to native species.

Keywords: Carnivore, coyote, gray fox, invasive, red fox, San Francisco Bay, Vulpes vulpes.

Introduction

Red foxes (*Vulpes vulpes*) are the most widespread non-domesticated carnivore in the world, and have been enormously successful at invading many habitats (Larivière and Pasitschniak-Arts 1996). They occur on six continents and have continued to increase their range over the last century (Lewis and others 1993; MacPherson 1964; Marsh 1938). Red foxes have also had tremendous impacts on native fauna in areas where they have been introduced; in Australia their arrival is linked to the decline and local extirpation of many native prey species (Burbidge and Manly 2002, Burbidge and McKenzie 1989, Dickman 1996, Kinnear and others 1988, Kinnear and others 1998).

Non-native red foxes were introduced into lowland California in the late nineteenth century for fur farming and hunting. A localized population of these animals in the Sacramento Valley was first described by Grinnell and others (1937), who believed them to be distinct from the native Sierra Nevada red fox (*V. v.*

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[2] Graduate Student and Professors, respectively, Department of Environmental Science, Policy and Management, University of California, Berkeley, CA 94720. e-mail: abidlack@nature.berkeley.edu; adina@nature.berkeley.edu; getz@nature.berkeley.edu.

necator). Residents from five counties described hunting and trapping these valley foxes beginning in about 1896 (Grinnell and others 1937). Foxes were also imported and released in Orange County for hunting from 1905 to 1919 (Sleeper 1987). Commercial fur farming became very popular in the mid-twentieth century, with approximately 125 fox farms throughout California by the early 1940s (Vail 1942), and many foxes undoubtedly escaped or were released from these farms (Lewis and others 1993). Gray (1975) documented red foxes occupying 16 counties in Northern California, with most sightings occurring in the Sacramento Valley. Gray (1975) also described a population from Los Angeles County, and stated that there were unconfirmed sightings in other Southern California localities. Most recently, Lewis and others (1993) documented the presence of red foxes in 36 counties throughout the state, excluding the North Coast, the Modoc Plateau, and the Mojave Desert.

Red foxes have been implicated in the decline in California of several federally threatened and endangered bird species, including the light-footed clapper rail (*Rallus longirostris levipes*), the California clapper rail (*R. longirostris obsoletus*), the California least tern (*Sterna antillarum browni*), and the western snowy plover (*Charadrius alexandrinus nivosus*; U.S. Fish and Wildlife Service 1990; U.S. Fish and Wildlife Service and U.S. Navy 1990). While depredations of bird populations have been well-documented, less is known about red fox impacts to mammalian prey species and native carnivores. Anecdotal evidence suggests that red foxes have replaced gray foxes (*Urocyon cinereoargenteus*) in some areas (J. Patton and R. Barrett, pers comm), and that when red fox numbers are reduced, gray fox populations rebound (J. DiDonato, pers comm). Red foxes have also killed several federally endangered San Joaquin kit foxes (*Vulpes macrotis mutica*; Clark 2001; Ralls and White 1995), and there is concern over possible introgression between non-native red foxes and the Sierra Nevada red fox (Perrine 2005).

Red foxes are often associated with human-dominated landscapes and may sustain very high densities in these heterogeneous habitats (Catling and Burt 1995; Kurki and others 1998; Larivière and Pasitschniak-Arts 1996; Oehler and Litvaitis 1996). In urban Orange County, red foxes utilize open spaces such as golf courses, airports and cemeteries (Lewis and others 1993). In North America, predation and competition by coyotes (*Canis latrans*) may also be important in shaping red fox distributions (Harrison and others 1989; Sargeant and others 1987; Sargeant and Allen 1989; Voigt and Earle 1983). Coyotes tend to avoid urban or developed areas (Gosselink and others 2003; Odell and Knight 2001), and these regions might provide a refuge from coyote predation for red foxes.

Since the mid-seventies, non-native red foxes have been present and locally increasing in number around the San Francisco Bay (J. DiDonato, pers comm.; Lewis and others 1993). Counties surrounding the Bay Area support a diverse mix of high- and low-density housing, vineyards, oak woodlands, and grasslands, resulting in a complex interface between human-dominated landscapes and wildlands. However, most of the undeveloped land is under private ownership and is subject to intense vineyard and residential development pressure. If red fox dispersal and successful establishment is predicated on landscape conversion, these development pressures may lead to the continued red fox invasion of northern coastal California oak woodlands. Our objective was to evaluate the abundance of red foxes in oak woodlands in Contra Costa and Alameda counties, in order to assess the extent of their spread from human-dominated habitats into wildlands in the East Bay.

Methods

We used a geographic information system (GIS) to select core oak woodland sites in Contra Costa and Alameda counties. Using the State of California Fire and Resource Assessment Program vegetation classification layer, along with the Bay Area Open Space Council open space layer, we examined the land cover within a 5 km^2 circle around the centroid of each open space polygon. We defined core woodland areas as those circles that contained 25 percent to 75 percent combined hardwood, conifer and shrub cover, of which at least 50 percent was hardwood. These constrictions ensured that grasslands and closed-canopy forests were not included in our site selection and that any cover was predominantly hardwood rather than shrub or conifer. We also eliminated properties with greater than 5 percent water, wetland, urban, or agriculture area. This provided us with 15 oak woodland dominated properties, under a variety of ownerships, for which we eventually obtained permission to survey 12. Six of these properties were sufficiently large enough to conduct two survey transects, making a total of 18 transects (*fig*. 1).

Surveys for red fox were performed using a detection dog trained to locate the scats of all canids and felids, excluding domestic dog. Scat sniffing dogs have proven to be both remarkably efficient and precise in their searching. In prior research, detection dogs have correctly identified 100 percent of target carnivore scats in a matrix of sympatric species (Smith and others 2001, 2003) and have detected the

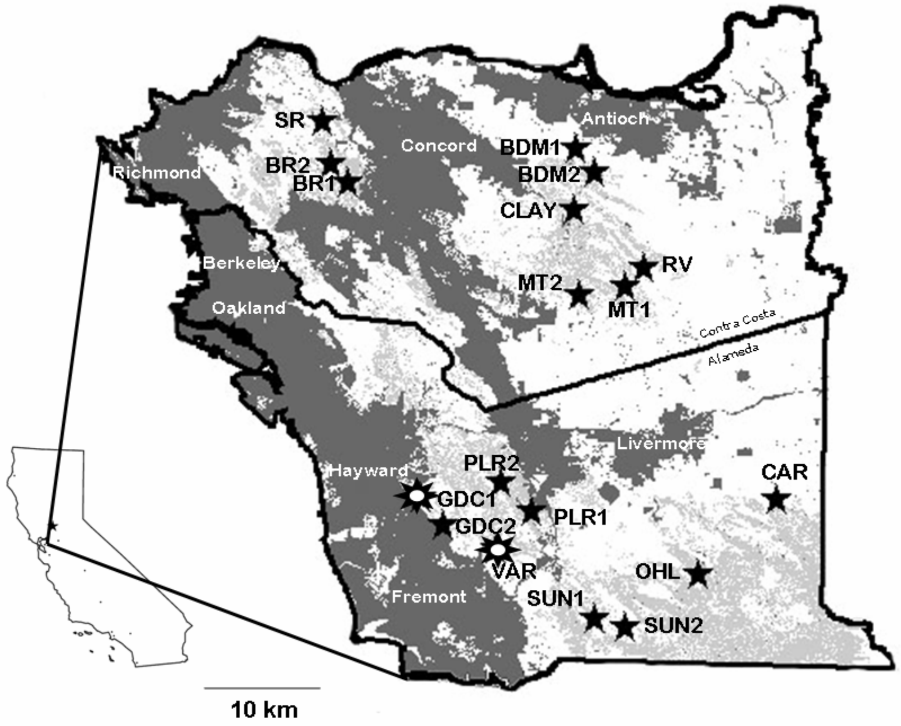

Figure 1—Location map of survey transects in the East Bay. BDM1 and BDM2, Black Diamond Mines Regional Park; BR1 and BR2, Briones Regional Park; CAR, Carnegie State Vehicular Recreation Area; CLAY, Clayton Land Bank; GDC1 and GDC2, Garin/Dry Creek Regional Park; MT1 and MT2, Morgan Territory Regional Park; OHL, Ohlone Wilderness; PLR1 and PLR2, Pleasanton Ridge Regional Park; RV, Round Valley Regional Park; SR, Sky Ranch; SUN1 and SUN2, Sunol Regional

Wilderness; and VAR, Vargas Land Bank. Sunburst symbol represents sites where red foxes were found. Dark gray color represents urban areas, light gray is oak woodlands.

presence of target species regardless of species density or vegetation type (Smith and others 2005). In a controlled test, our dog detected 100 percent of scats placed within 10 m of the centerline of a transect along an unpaved road, and 98 percent of scats within 20 m (Reed and Bidlack 2006). A pilot survey indicated that in these oak woodland systems, most canid scats are deposited along trails, with surveying and collection off-trail extremely difficult and inefficient (Bidlack Unpublished data). Therefore, surveys were conducted along fire roads, and hiking and game trails. Transect start points and direction were chosen randomly within the site, which means that the land cover around the transect may differ slightly from that around the centroid of the site. Each transect was 2-km long, and all transects were separated by at least 2.5 km to increase independence of sampling (red fox home ranges vary widely, but average 5 square km [Larivière and Pasitschniak-Arts 1996]). Due to time and financial constraints, each transect was surveyed only once.

Collected scats were individually bagged and given an identification number and a GPS location and subsequently stored at -80^0 C. Scats were later identified to species using molecular genetic methods. DNA was extracted from each scat using a small sub-sample (~500 g) that was removed from the outer surface or end of each feces and used in a QIAamp DNA stool kit (Qiagen). Polymerase chain reaction (PCR) was then used to amplify a 196 base pair segment of the mitochondrial cytochrome *b* gene. Restriction fragment length polymorphism (RFLP) analysis using three restriction enzymes (*Hpa*II, *Dde*I and *Hpy*Ch4V) to cut this fragment was used to separate coyote, gray fox, red fox, and bobcat scats (for protocols see Bidlack and others 2006).

Results and Discussion

Eighteen 2-km transects were surveyed during the summer of 2005. We collected a total of 383 scats, with a mean of 21.3 scats found per transect, and with a range of 5 to 48. There was a mean of 12.48 (± 8.83 s.d.) scats located per km. Using molecular methods we identified 353 scats (92 percent) to species. Coyote scat was the most prevalent at 222 (62 percent), followed by gray fox at 93 (26 percent), bobcat at 35 (10 percent), and red fox at three (1 percent). Coyotes were detected at all sites, while bobcats and gray fox were detected at 11 and 7 sites, respectively. Red fox scats were found at only two sites, Vargas Plateau and Garin/Dry Creek, both in Alameda County (fig. 1).

Our study indicates that red foxes have not been particularly successful in invading core oak woodlands in the East Bay. This may be the result of several factors, one of which is the amount and pattern of development. Most previous research in other regions suggests that red foxes are closely associated with disturbed or heterogeneous habitats. In Australia, red foxes only occur in forested patches close to areas that have been cultivated, heavily grazed, burned, logged, or converted to residential development (Catling and Burt 1995). In Europe, red foxes are most abundant in landscapes including 20 to 30 percent agricultural land (Kurki and others 1998). Urban areas may provide reliable sources of food, water, and cover for foxes; in fact, local residents provided red foxes with supplemental food at every site studied in Orange County (Lewis and others 1993). The two sites in which red fox scats were found in our study were both near developed areas. Vargas Plateau is a working cattle ranch, and Garin/Dry Creek Park directly abuts a dense residential neighborhood, unlike all the other sites (some of which are adjacent to low-density suburban developments). Another recent survey for foxes conducted in grasslands (<25 percent canopy cover) in eastern Alameda and Contra Costa counties indicates that red foxes may persist only near permanent water sources such as reservoirs and canals (Clark and others 2003; Smith and others 2006). This study surveyed 17 sites in these two counties and detected red foxes at only three sites, again confirming that this species has on the whole not been successful in invading wildlands in Northern California (Clark and others 2003; Smith and others 2006). Red foxes may not be able to persist in wildlands far from developed areas, though they may survive in the same types of habitats close to human development. This pattern has been observed in other human-associated species (for example, domestic cats, cowbirds; Hejl and others 2002; Maestas and others 2003; Morrison and Hahn 2002; Odell and Knight 2001). If red fox occupancy patterns reflect a reliance on human development, then conserving large patches of undeveloped oak woodland habitat in the East Bay may help buffer these habitats against invasion by red fox.

The high numbers of coyotes in the East Bay may also be excluding red foxes from some areas, or keeping their abundance low. Coyotes are known to kill red foxes (Sargeant and Allen 1989), and red foxes will avoid areas with high densities of coyotes (Harrison and others 1989; Sargeant and others 1987; Voigt and Earle 1983). We found coyote scats on all of our transects, indicating that they are ubiquitous in oak woodlands in the Bay Area. We found no relationship between coyote abundance and distance of the transect from developed areas. However, we found coyote scats on the same transects with red fox scats. Currently, the relationship between these two species is still unclear, and it is impossible to differentiate between coyote presence and lack of development as impediments to red fox spread into core woodlands. Similarly, we remain uncertain concerning the interaction between gray and red foxes in these sites, in view of the fact that we found gray fox scats at both of the sites that also supported red fox.

Recently, presence/absence surveys have come under criticism for a general lack of detection rate estimates, leading to biased approximations of habitat occupancy (MacKenzie and others 2006, and papers cited therein). However, surveys performed by scat detection dogs are likely to detect more species and more samples per species, especially for rare taxa, than other non-invasive survey methods such as searching by humans, track plates, remote cameras, and hair snares (Harrison and others 2002; Smith and others 2001). We made the assumption that all species were defecating on roads and trails, and that there would be no detection bias by the dog among the target species. Our findings concerning red fox occurrence are corroborated by the results of Smith and others (2006), who surveyed some of the same properties (Black Diamond Mines, Round Valley, Carnegie State Recreation Area) using a scat-detection dog, with negative results. Nevertheless, our surveys may be an underestimate of species presence, given that transects were only surveyed once.

Our preliminary data suggest that in the East Bay red foxes have successfully established populations only in core oak woodlands adjacent to human development. Further research is needed to better quantify the habitat correlates of red fox as well as to tease apart the relationships among the three canid species in the area. In this way we may gain insight into the drivers of the red fox invasion, and the possible impact of future development on the spread of this exotic species.

Acknowledgments

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Continue

The Impact of Imported Water on Hardwoods Range Ecosystems[1]

Thomas Scott[2]

Abstract

Water Pollution is defined as the corruption of ecosystems, human health, and local economies by the inappropriate introduction of contaminants into water-ways. Although counter-intuitive, water itself has become a pollutant in California's hardwood rangeland, with ecological consequences that exceed the impacts predicted by models of global climate change. The greatest manifestations of this problem are year-round flows of surface water in streams that previously dried-out in summer months. The primary cause is excess and inefficient irrigation of suburban landscaping, which is often applied at rates equivalent to 50 inches of annual rainfall. Increases in summer flows at USGS gauging stations can be correlated with housing construction in areas like the Santa Clarita Valley, creating entirely new types of woodland ecosystems along the wildland/urban interface. These dysfunctional wetlands create a link between human and wildland ecosystems, putting both human and wildlife populations at risk. Although many of these woodland ecosystems are less than 20 years old, they played a major role in the spread of West Nile Virus and could play a role in the spread of Bird Flu, Dengue fever, and Malaria.

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[2] IHRMP, University of California, Berkeley. e-mail: Thomas.Scott@ucr.edu.

Continue

California Oaks and Fire: A Review and Case Study[1]

Katherine A. Holmes,[2, 3,] Kari E. Veblen,[2, 3] Truman P. Young,[2, 3] and Alison M. Berry[2, 3]

Abstract

California has a fire-prone Mediterranean climate, and many of its nine species of native oak trees are thought to have evolved with fire. Little has been widely published about the role of fire in the oak recruitment and mortality in the western United States, and there has been some debate about how to reintroduce fire into oak woodlands. We present here a review, synthesis, and analysis of the literature on fire and California oak species. This literature review suggests high overall survival of oaks after fire, although smaller individuals often experience topkill (death of all above-ground stems, followed by recovery via sprouting of basal shoots from the root crown). We then provide results from a case study of a controlled burn on the survival of 5-year-old valley oaks (*Quercus lobata*) at a restoration research site near Davis, CA. One-half of the trees at our site were exposed to a set of prescribed burns in summer 2003, and another half were left unburned as a control. Prior to burning, measurements were taken on each tree's height, diameter, and understory grass biomass. Fire temperatures were measured using temperature-sensitive paints on ceramic tiles hung on each tree. Only 3 percent of the oaks died as a result of the fire, although 85 percent were topkilled. Smaller trees, trees exposed to higher fire temperatures, and trees with higher levels of understory biomass suffered more damage. About one-third of trees over 200 cm tall escaped being topkilled. Our investigation of the effects of fire on young valley oak trees indicates that saplings of this species, similar to the saplings of most western oak species, are resilient to fire, especially if managers are willing to accept the temporary setbacks associated with topkill.

Keywords: Basal sprout, coppice, prescribed burn, prescribed fire, Quercus lobata, *topkill, valley oak, wildfire.*

Introduction

California has a fire-prone Mediterranean climate, and many of its nine species of native oak trees are thought to have evolved with fire (Pavlik and others 1991). Native Americans were known to set fires in many oak communities, and fires before the mid-1800s were probably fairly frequent and of low intensity (Lewis 1982). With the advent of the gold rush in 1848, fires in California initially increased in frequency and then, starting in the 1940s, were almost completely suppressed (Biswell 1989, McClaran and Bartolome 1989).

Some of California's oak communities have not been experiencing normal recruitment in recent decades; although oak stands contain many mature individuals, young trees and saplings are often rare or absent (Bolsinger 1988, Griffin 1976). It may be that changes in California's fire regime have contributed to this lack of regeneration, although there are other potential causal factors, including increases in deer and rodent populations and the introduction of domestic livestock and invasive

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2 Department of Plant Sciences, University of California, One Shields Avenue, Davis, CA 95616. e-mail: holmeska@sbcglobal.net.

3 Ecology Graduate Group, University of California, One Shields Avenue, Davis, CA 95616.

annual plants (Pavlik and others 1991). Little is known about the role of fire in oak recruitment and mortality (Barbour and Minnich 2000), and there has been some debate about the proper way to reintroduce fire into oak woodlands (Bartolome and others 2002, Biswell 1989).

The effect of fire on valley oak trees (*Quercus lobata*) is of particular interest to restoration efforts in California's Central Valley. Valley oak trees are the dominant members of California's low-elevation riparian oak woodlands (Pavlik and others 1991), and are some of the most threatened communities in California because of flood control and agriculture activities (Vaghti and Greco *in press*). It is estimated that only 6 percent of the historic riparian forest remains in California's Central Valley (Katibah 1984). Many restoration efforts focus on valley oak restoration, and it is one of the most frequently planted trees at restoration sites in the Central Valley (Young and Evans 2005). Newly-restored valley oak communities often have serious invasions of understory non-native grasses and thistles. Although prescribed burning can be an effective control for these exotics, managers may be reluctant to use fire if it causes substantial mortality of sapling valley oak trees.

We reviewed and analyzed the literature on fire and California oak species. Although some species have been investigated in a number of studies, particularly blue oak (*Q. douglasii*) and coast live oak (*Q. agrifolia*), the effects of fire on other oak species, including valley oaks, have only been minimally addressed. We therefore present preliminary results from a case study of a controlled burn on valley oak saplings at a research restoration site near Davis, CA.

Statistical Review of Previous Research

We identified studies on the effects of fire on California oak species by searching the electronic database BIOSIS Previews with various combinations of the following keywords: oak*, lobata, valley oak*, burn*, fire*, prescribed, California, west*, and advance regeneration (where * is a truncation symbol). Proceedings from the 1979, 1986, 1990, 1996, and 2001 Symposiums on Oak Woodlands published by the USDA's Forest Service Pacific Southwest Research Station were also searched for relevant articles. As articles were identified for inclusion in our study, their cited literature was scrutinized for additional references. Although our statistical analysis was restricted to studies that investigated the effects of fire on oak species native to California, if relevant, results from other areas of North America are mentioned in the discussion.

A total of 14 studies on seven different species were identified, although three did not report data in a form that allowed for inclusion in our analysis. Many of the studies addressed multiple species and/or multiple sizes (seedling, sapling, mature); therefore, a total of 26 cases were included in our analysis. One-way ANOVAs or t-tests were used to analyze the effect of predictor variables (tree size, fire season, and oak species) with respect to tree response to fire (death or topkill). Homogeneity of variance was checked with Levene's tests and, if necessary, non-parametric tests were used.

Due to low replication of studies within species, it is not clear whether the differing results described in the following sections are due to differences in species, sites or experiments. Nonetheless, some consistent patterns emerge.

Potential Benefits

Fire may reduce competitive pressures from species that are more fire-sensitive than oaks. Managers of senescent oak forests in the southeastern United States have long used prescribed burning to reduce the densities of certain oak competitors, such as maple (*Acer*) and gum (*Nyssa*) trees (Arthur and others 1998). These species have come to dominate their communities with the advent of fire suppression, and prescribed fire restores oak dominance (McCarty 1998). Many non-native understory species have invaded oak woodlands, particularly in California, and fire has been used as a restoration tool to control common understory exotics, such as Scotch broom (*Cytisus scoparius*), yellow star thistle (*Centaurea solstitialis*), and various annual grasses (Bossard and others 2000).

Fire may promote acorn germination and growth, possibly by reducing competitive pressure from understory vegetation, releasing soil nutrients, reducing litter-born pathogens, or improving contact with mineral soils. Kauffman and Martin (1987) found that densities of black oak (*Q. kelloggii*) seedlings were up to nine times greater in burned plots than unburned plots. Oregon white oak (*Q. garryana*) acorns planted in fire-charred soil had a significantly higher emergence rate than those planted in unburned soil (Regan and Agee 2004). No similar increase in recruitment, however, was found for acorns of blue oak (Allen-Diaz and Bartolome 1992) or valley oak (Swiecki and Bernhardt 1998).

There may also be broader community benefits to burning. Haggerty (1994) noted that the previously abundant oak mistletoe (*Phoradendron villosum*) was completely eliminated after a wildfire in a stand of blue oak and interior live oak (*Q. wislizeni*), suggesting that the current abundance of mistletoe may be an artifact of fire suppression. Dagit (2002) found an increase in native species' cover in the understory of a coast live oak woodland after a wildfire, although natives were gradually being replaced by exotics as time since fire increased. More research on such effects is needed.

Potential Risks

Many species of mature oaks are relatively tolerant to fire. However, even large oaks can die as a result of fire exposure, and sapling and seedling oaks are at greater risk. Our survey of studies investigating the effects of fire on California oak species found that mortality rates generally ranged between 1 to 11 percent for mature oaks, 2 to 10 percent for sapling oaks, and 17 to 52 percent for seedling oaks (*table 1*). Larger trees were significantly more likely to survive fire than were smaller trees and seedlings (Wilcoxon $p = 0.01$, *fig. 1*).

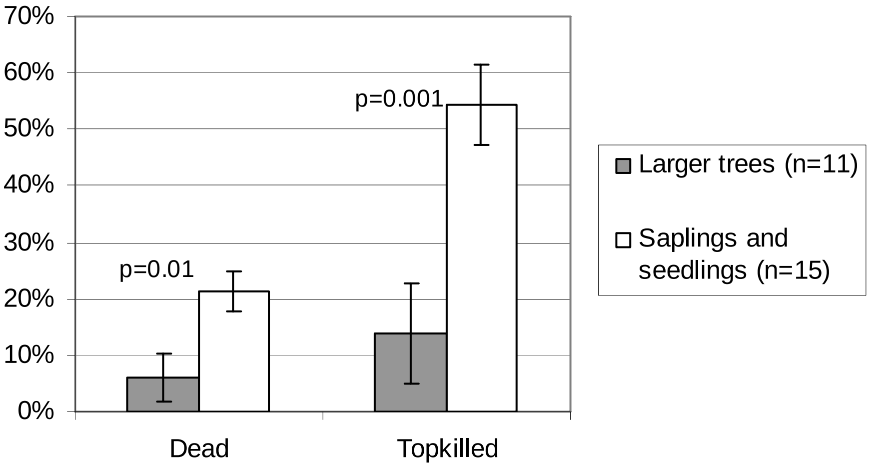

Figure 1—Comparison of death and topkill rates between large and juvenile oaks exposed to fire, based on a review of the literature (*table 1*). Bars represent one standard error. Sample sizes are the number of cases in each size class.

Even though fire does not usually completely kill sapling oaks, it topkills them 75 to 90 percent of the time (*table 1*). "Topkill" means that the above-ground portions of an individual sapling die, but that recovery occurs via sprouting of new basal shoots (coppices) from the tree's root crown. Two studies of seedling oaks exposed to fire (Schwan and others 1997, Lathrop and Osborne 1991) reported topkill levels from five to 52 percent – levels much lower than those found for sapling trees. It is hard to determine the topkill status of very small oaks because their branches are small enough to be completely consumed by fire, and subsequent regrowth makes it difficult to find evidence of a dead main leader (personal observation). It may be that in some cases the topkill rates reported for seedling oaks are artificially low due to the difficulty of distinguishing dead main leaders.

In our sample of studies, saplings and seedlings were significantly more likely to be topkilled by fire than were larger trees (t-test p = 0.001, *fig. 1*). Topkilled trees, although often capable of complete recovery, may be more susceptible to further damage from deer browsing or subsequent fires until the basal shoots grow up through susceptible height classes (Bartolome and others 2002, Swiecki and Bernhardt 2002).

Fire Characteristics

Several different fire characteristics can influence the damage and mortality response of oak trees, including fuel load, fire frequency, and fire season. The amount of understory litter, brush, and downed wood (fuel load) is often high in areas with low fire frequency, and differences in fuel loads can have a dramatic effect on fire damage. Fire-induced mortality in black oak stands with high fuel loads was about twice that of moderate-fuel load areas (Kauffman and Martin 1987). Blue oak saplings were significantly more likely to escape being topkilled if they were located in areas with light fuel loads, rather than medium or heavy fuel loads (Tietje and others 2001).

In other parts of the United States, multiple fires within a short period of time have been found to increase oak mortality rates (Dey and Hartman 2005, Peterson

Table 1—*Summary of research publications on the effects of fire on California oak species.*

Species	#	Fire type/season	Dead	Topkilled[a]	Citation
Mature trees					
Q. agrifolia	90	wildfire, Nov	4%	not specified	Dagit 2002
Q. douglasii *Q. kelloggii* *Q. lobata*	208	prescribed, June	1%[b]	none noted	Fry 2002
Q. douglasii	119	wildfire, June	6%	8%	Haggerty 1994
Q. wislizeni	29	wildfire, June	11%	24%	Haggerty 1994
Mixed-age					
Q. agrifolia (>7.5cm dbh)	165	wildfire, Aug	5%	11%	Plumb 1980
Q. chrysolepis	239	prescribed, Nov	<15cm dbh 47%[c] >15cm dbh 10%[c]	included in dead	Paysen and Narog 1993[d]
Q. chrysolepis (>7.5cm dbh)	156	wildfire, Nov	2%	63%	Plumb 1980
Q. douglasii	100	wildfire, summer	2%[b]	seedling 50% others 8%	Horney and others 2002
Q. garryana	874	prescribed, spring prescribed, fall prescribed, 2x	spring 94/ha[c] fall 91/ha[c] 2x 523/ha[c]	included in dead	Regan and Agee 2004 [d]
Q. kelloggii	?	prescribed, various	high fuel 55-91% mod. fuel 22-65%	none noted	Kauffman and Martin 1987 [d]
Q. kelloggii	72	wildfires, various	13%	24%	Plumb 1980
Q. lobata	266	wildfire, Aug	20%	not specified	Griffin 1980
Saplings					
Q. agrifolia	90	wildfire, Aug	2%	88%	Plumb 1980
Q. agrifolia	18	prescribed, Oct	<5%	74%	Tietje and others 2001
Q. chrysolepis	10	wildfire, Nov	10%	90%	Plumb 1980
Q. douglasii	38	prescribed, Oct	<5%	78%	Tietje and others 2001
Q. douglasii	67	wildfire, Sept	9%	82%	Swiecki and Bernhardt 2002
Q. douglasii	48	prescribed, July	<10%	>90%	Bartolome and others 2002
Seedlings					
Q. agrifolia	89	prescribed, June prescribed, Nov	June 46% Nov 52%	June 50% Nov 36%	Lathrop and Osborne 1991
Q. agrifolia[e] *Q. douglasii*[e] *Q. lobata*[e]	558	wildfire, July	QUAG 44% QUDO 17% QULO 17%	5%[b]	Schwan and others 1997
Q. engelmannii	699	prescribed, June wildfire, Aug prescribed, Nov	June 45% Aug 34% Nov 22%	June 53% Aug 52% Nov 50%	Lathrop and Osborne 1991

[a] Death of all above-ground stems, followed by recovery via sprouting of basal shoots.

[b] Study addressed either multiple species or multiple sizes of oaks; results not provided individually.

[c] Topkilled trees included in numbers reported for dead trees.

[d] Study did not report data in a form that allowed for inclusion in statistical analysis.

[e] Most trees in study were seedlings, although some sapling–sized trees were also included.

and Reich 2001). Hutchinson and others (2005), however, found lower mortality at more-frequently burned sites, perhaps because their more-frequently burned sites experienced lower-intensity fires. Regan and Agee (2004) found that two prescribed burns in Washington within a 5-year period increased Oregon white oak mortality more than five-fold over single burns. We found no studies on the effects of multiple fires on oaks in California.

The seasonal timing of fires is also believed to affect the extent of tree damage. Increased susceptibility to summer fires may be because higher ambient temperatures cause internal tree temperatures to increase to mortal levels during fire much more rapidly than do lower ambient temperatures (Hare 1965) or because low fuel moisture creates more intense fire conditions (Whelan 1995). Some trees may be more sensitive to spring fires, however, because higher moisture content in bark can increase thermal conduction (DeBano and others 1998). It is likely that historical fires in California were more likely to occur in the late summer and fall (Lewis 1985). Many controlled burns now occur in the spring and early summer, either to better kill non-native weeds or to provide more controlled conditions for fires.

Only a few studies have specifically addressed burn response by season, and their results have been somewhat conflicting. Ferguson (1957) found that several Texas oak species were more likely to survive winter or spring burns than summer burns, as have studies from the eastern United States (Brose and Van Lear 1998, Cain and Shelton 2000). In contrast, Lathrop and Osborne (1991) found that Engelmann oak (*Q. engelmannii*) seedlings in Southern California had higher survival rates for both summer and fall burns compared with a spring burn. Although the trend was for late-season burns to have more severe impacts than spring burns (*fig. 2*), the studies of California oak species we reviewed showed no significant differences among burn seasons in either mortality (ANOVA p = 0.98) or topkill (ANOVA p = 0.13).

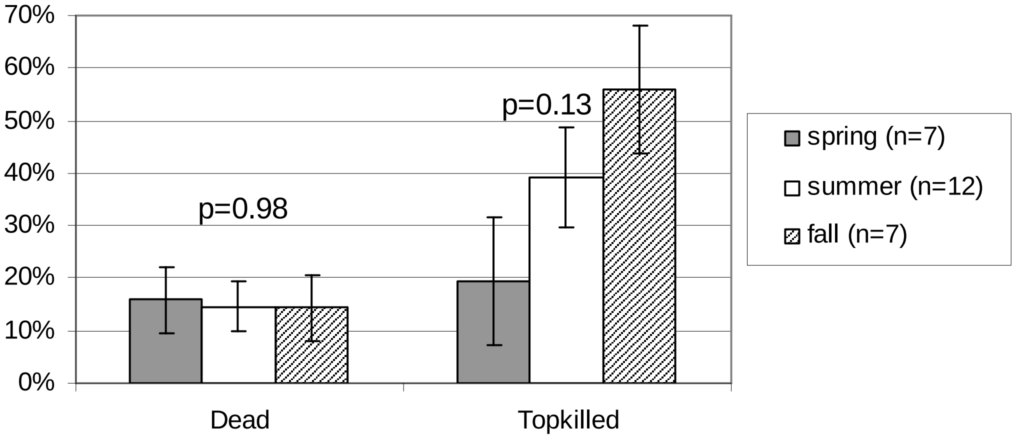

Figure 2—Comparison of death and topkill rates of oaks after fires that occurred at different times of year, based on a review of the literature (*table 1*). Bars represent one standard error. Sample sizes are the number of cases in each season class.

Species-Specific Fire Response

Fire response appears to vary among California's oak tree species. Plumb (1980) found that coast live oak tolerated fire better than black oak, while canyon live oak (*Q. chrysolepis*) was extremely fire sensitive. Blue oak has been shown to be more fire resistant than interior live oak (Haggerty 1994), and Engelmann oak is more resistant than coast live oak (Lathrop and Osborne 1991). Differences in bark are posited to be the primary factors responsible for varying fire responses among tree species (DeBano and others 1998). Several bark characteristics, including increased thickness, non-flaky texture, and high density, reduce the negative effects of fire by minimizing heat transmission to the underlying cambium cells (Hare 1965, Plumb 1980). Snow (1980) found that Engelmann oak seedlings recovered from fire faster than coast live oak seedlings. He identified Engelmann oak's bark thickness, which was twice that of coast live oak's, as the likely explanation.

Our review of seven different California oak species (black, blue, canyon live, coast live, Engelmann, interior live, and valley) found no significant difference in either death (Kruskal-Wallis $p = 0.32$) or topkill (Kruskal-Wallis $p = 0.24$). However, this is likely due to the low replication of case studies within species (three or less for five of the seven species), which limited our ability to separate species effects from the effects of other differences in individual studies.

Prediction of Survival

Logistic regression and discriminant analysis models have been used to predict which oak trees will be damaged or killed by fire. Some of the tree characteristics analyzed include height, diameter, crown height, crown width, and bark thickness. Most studies have found that larger, older trees are significantly less likely to be damaged by fire (Fry 2002, Horney and others 2002, Paysen and Narog 1993, Regan and Agee 2004, Swiecki and Bernhardt 2002), although one study of wildfire in a mature stand of blue and interior live oaks found no significant difference attributable to tree size (Haggerty 1994). Swiecki and Bernhard (2002) used their model to propose critical threshold levels, suggesting that blue oak saplings more than 2-meters tall are likely to avoid being topkilled by fire, while those under 1-meter tall are more likely to be completely killed. Increase in fire damage (parameters analyzed include percent bole char, height of bole char, char severity, and percent crown scorch) has also been found to be predictive of subsequent topkill and mortality (Fry 2002, Haggerty 1994, Horney and others 2002, Paysen and Narog 1993, Regan and Agee 2004).

Recovery of Height

Results from several studies indicate that blue oak saplings topkilled by fire can experience a period of accelerated growth from one to several years after the fire. That growth significantly exceeds the growth of less damaged or unburned trees (Bartolome and others 2002, McClaran and Bartolome 1989, Swiecki and Bernhardt 2002). Schwan and others (1997) found accelerated growth in coast live oaks after a wildfire, although growth of valley and blue oaks was stagnant or negative. Studies of oaks in the eastern United States have found evidence of increased postfire growth (Brose and Van Lear 1998). In most cases, however, accelerated growth has not resulted in burned trees returning, within a few years, to the full height they would have been had they not been burned (in other words, not full compensation). In a

Missouri forest with dense canopy cover, lack of height recovery was presumably due to shading from overstory trees, which reduced photosynthesis (Dey and Hartman 2005). Slow height recovery has also been found in areas with large deer or livestock populations, since topkilling returns saplings to heights accessible to browsing animals (Bartolome and others 2002, McClaran and Bartolome 1989).

A Case Study: Effects of a Prescribed Burn on Valley Oak Saplings of Different Sizes

Our review of the literature on fire and California oak trees revealed that very few studies have examined the effects of fire on valley oak trees in general, and none have comprehensively addressed sapling-aged valley oaks. This is unfortunate, since prescribed fire can be an important management tool at restoration sites in the Central Valley, many of which include newly planted valley oaks. Fire effectively controls exotic annual grasses and thistles, but can be used only if young valley oaks are reasonably fire-tolerant. In light of the potential for differences in species-specific fire response, more study on the effect of fire on young valley oaks is needed. We conducted a prescribed burn in a field of sapling valley oaks for the purpose of (1) investigating valley oak response to prescribed fire; (2) determining critical thresholds for mortality and topkill; and (3) identifying factors that are predictive of fire response.

Methods

Our study site is a 2-hectare research field near Davis, California. The site was planted with several hundred valley oak acorns and seedlings in the winter of 1999 as part of an unrelated restoration experiment (Hobbs and Young 2001, Young and Evans 2001, 2005). The original experiment concluded in 2001, and 278 trees remained at the site by summer 2003. None of the trees received supplemental irrigation after summer 2000. There is no overstory canopy layer at the site, and the understory layer is dominated by nonnative annual grasses (*Bromus*, *Avena*, *Lolium*, and *Hordeum* species) and yellow star thistle.

The site was subdivided into plots of approximately 72 m^2 each, with an average of 10 trees per plot. Nine plots were burned in the summer of 2003 and nine were left unburned as a control. The plots assigned to burning treatment were regularly interspersed with the controls. Each plot had oaks that differed substantially in size, and our analysis combined all trees of a particular height, across all plots. There were substantial differences in tree size due to the previous restoration experiment, and plots were stratified to more evenly distribute tree size.

In April 2003, the height and stem diameter at 30 cm was measured for each tree. For those trees in the burn treatment, the grass biomass under each tree was assigned a density level of one (low) through three (high). Ceramic tiles painted with six different temperature-sensitive welding paints (ranging at regular intervals from 79 ˚C to 399 ˚C) were hung at a height of 30 cm on each tree. Three weeks after the burn, the height of the top of the scorch level was measured for each tree. Three months after the burn, the survivorship of each tree’s main leader was assessed, and the number of basal sprouts and height of the tallest sprout were measured.

The burn was conducted on July 16, 2003, from 12:00 p.m. until 4:00 p.m. Dry bulb temperatures averaged 34 ˚C during the burn and relative humidity was 37 percent. As recorded by the ceramic tiles, fire temperatures reached a high of 204 ˚C with a mean of 95 ˚C. Most of the litter and understory herb layer was consumed in the fire, although some patchiness was evident with small areas of litter only lightly charred. Fire carried into the crowns of many of the saplings, and 26 percent of them experienced 100 percent crown scorch, although leaves and small twigs were only rarely completely consumed by the fire.

Results

The burn resulted in three levels of tree response, with the most severe being entire tree death, followed by topkilled trees with dead main leaders but vigorous sprouting from the root crown, and trees whose main leaders survived (*table 2*). Only three percent of the valley oak saplings died as a result of the fire; however, 85 percent of the burned trees were topkilled. Two years after the fire, most of the burned trees appeared quite robust, and even the topkilled trees were approaching the height of the control trees.

Table 2 — *Proportions of valley oak saplings in each treatment, by fire response*

	Trees in burned plots	Trees in unburned plots
Dead	0%	3%
Topkilled, coppicing	0%	85%
Alive	100%	12%
N	96	88

Tree height, fire temperature and understory biomass density all contributed to the severity of tree response to fire. Smaller trees, trees exposed to higher fire temperatures, and trees surrounded by denser understory biomass were more likely to experience death or topkill in response to the fire (*figs. 3, 4, 5*). All three trees that died in the fire were under 150-cm tall. Although there were no height classes that completely avoided being top-killed by the fire, increasing proportions of trees above 200 cm escaped topkill. In the largest height class (251-350 cm), one-third of the trees avoided being topkilled.

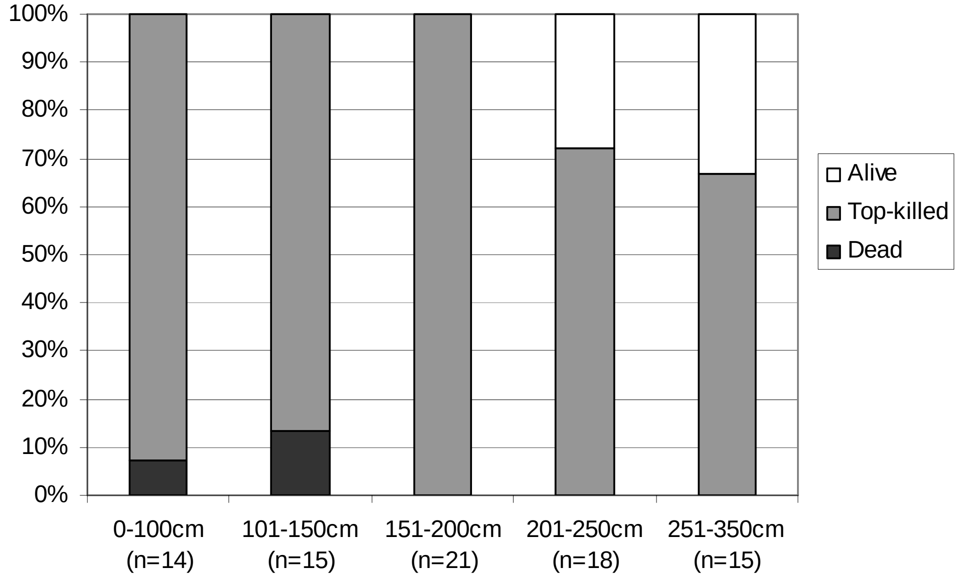

Figure 3—The proportions of valley oak saplings of different heights that experienced different fates after a prescribed burn. Sample sizes are the numbers of individual trees in each height class.

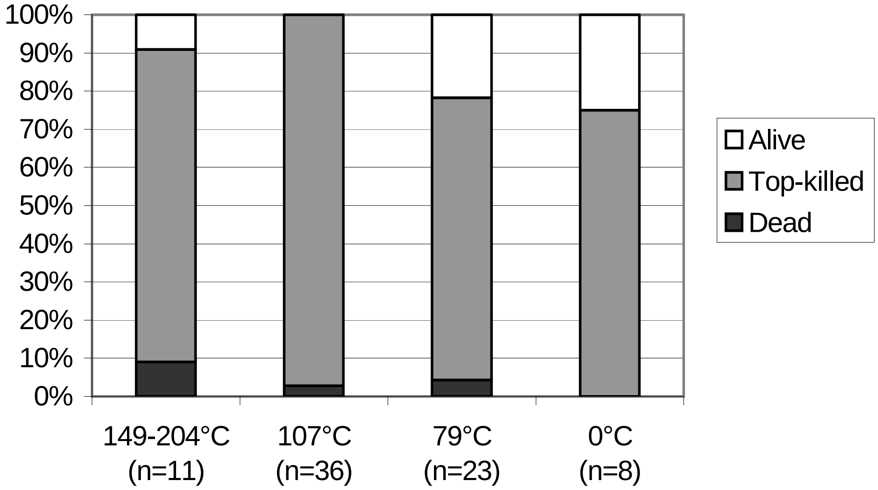

Figure 4—The proportions of valley oak saplings exposed to different minimum fire temperatures that experienced different fates after a prescribed burn. Sample sizes are the numbers of individual trees in each temperature class.

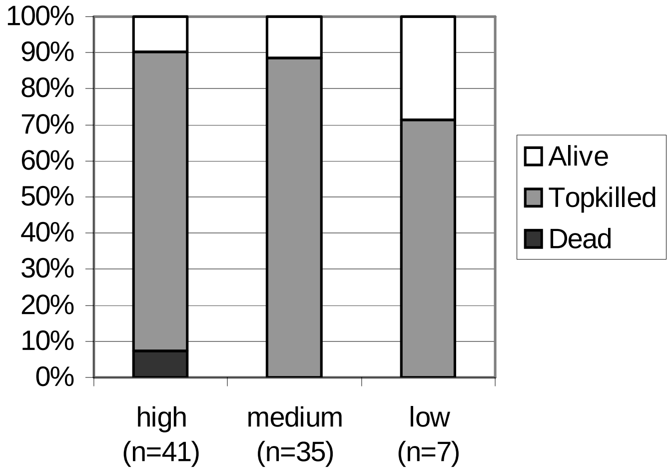

Figure 5—The proportions of valley oak saplings with different understory biomass density levels that experienced different fates after a prescribed burn. Sample sizes are the numbers of individual trees in each understory biomass density class.

Discussion

Our case study results indicate that valley oak saplings exposed to a low-intensity prescribed fire experience very low mortality rates but high topkill rates, similar to the fire responses found for several other sapling California oaks species. Three previous studies on other sizes of valley oak trees also found high survival after fire. A prescribed burn conducted by Fry (2002) in a mature stand of valley, blue, and black oaks resulted in less than 1 percent mortality. Griffin (1980) found a more variable response in a mixed-age stand of valley oaks exposed to wildfire; crown-fire killed 48 percent of the trees, severe ground-fire killed 18 percent, and moderate ground-fire killed 3 percent. Schwan and others (1997) studied the effects of a wildfire on 159 mostly seedling valley oaks and found a 17 percent mortality rate but only a 5 percent topkill rate. We have found that it is difficult to determine the topkill status of very small valley oaks, since the main leader is likely to be consumed by fire and the regrowth is rapid and vigorous. It may be that the topkill rate reported by Schwan and others was artificially low due to the small stature of their trees.

Although all three of the saplings completely killed by fire in our study were under 150-cm tall, most trees in the smaller height classes did not die. There does not, therefore, appear to be a critical height threshold for fire-induced mortality of valley oak saplings. Since none of our height classes reliably avoided being topkilled, we cannot propose a specific height above which valley oak saplings escape topkilling. Our data does show, however, that as saplings exceed 200 cm they become less likely to be topkilled.

Previous studies have identified several tree and fire characteristics that are predictive of oak trees' fire responses. Our case study found that tree size, fire temperature and fuel load all contribute to the severity of sapling valley oaks' fire response. Fire temperature and fire residency time are inversely proportional to each other in causing plant cell death (Bond and van Wilgen 1996), and cells can survive higher temperatures when the time of exposure is shorter. The larger saplings in our study presumably had thicker bark that more effectively insulated the underlying cambium layer, reducing the amount of time living cells were exposed to potentially lethal temperatures. Higher-density understory biomass not only provides more fuel, thereby increasing fire temperatures, but may also serve as a fuel ladder, carrying flames into tree crowns and increasing the potential severity of a fire's effects.

Two years after the fire, the trees burned in our experiment were approaching the height of unburned control trees and appeared healthy and robust. Our research site, although subject to rodent and hare herbivory, experienced very little deer browse pressure. Studies in areas with large deer or livestock populations have found that topkilled saplings experience slow height recovery because of browsing (Bartolome and others 2002, McClaran and Bartolome 1989).

Conclusion

Although there are some differences in fire sensitivity among oak species, most California oaks, even saplings, appear to be resilient in their ability to survive at least one-time burns, especially if managers are willing to accept the temporary setbacks associated with topkill. Land managers interested in using prescribed fire in young oak tree stands may want to minimize potential fire damage by addressing factors that have been shown to be predictive of severe fire response. Fire temperatures can be lowered by conducting burns when ambient temperatures are low and when relative humidity and fuel moisture is high; for example, either in early morning or early season. Understory biomass around sapling oaks can be reduced through the use of weed control fabric or via aggressive weed-whacking within the canopy line of individual sapling oaks immediately before burning.

Although the effects of fire on valley oak saplings has not been comprehensively addressed in previous research, the results of our case study indicate that valley oak saplings are capable of surviving fire with very little mortality and appear quite robust within a few years after fire. The presence of valley oak saplings does not therefore appear to preclude the use of a single low-intensity prescribed burn to control understory invasive plants in recently-planted restoration sites, particularly if the saplings are over 300-cm tall and measures are taken to reduce fire temperatures.

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Continue

Monitoring and Inventory

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1930s Extent of Oak Species in the Central Sierra Nevada[1]

James Thorne,[2] Jacquelyn Bjorkman,[3] Sarah Thrasher,[4] Ryan Boynton,[5] Rodd Kelsey,[6] and Brian Morgan[7]

Abstract

A major vegetation survey of California, the Wieslander Vegetation Type Mapping (VTM) Project, was conducted in the 1930s. Crews surveyed one-third of the state, recording detailed renditions of dominant vegetation patterns on topographic quadrangles. Documented on these maps are the dominant species of each vegetation polygon. We transformed 30,236 km^2 of the central Sierra Nevada VTM maps to digital format for use in Geographic Information Systems (GIS). We queried the resulting digital maps to develop maps of individual species in the genus *Quercus* for the region. This report presents the historical patterns and extents for five tree and four shrub species. We compared historical species' extents to modern extents, as measured by CalVeg, a modern digital vegetation map, for 16,978 km^2 of the study area. Results indicate a loss of 35 percent of historic blue oak habitat types, and an increase in montane hardwoods.

Keywords: Historic range map, landscape-scale, Quercus*, vegetation, Wieslander Vegetation Type Map.*

Introduction

The Wieslander Vegetation Type Map (VTM) Project was a United States Forest Service (USFS) effort to record California's vegetation between 1928 and 1940 (Griffin and Critchfield 1972, Wieslander 1935a, 1935b, 1985). Headed by Albert Wieslander, a silviculturist with the U.S. Forest Service California (now Pacific Southwest) Forest and Range Experiment Station, the group took more than 3,000 photographs of vegetation, surveyed more than 17,000 vegetation plots, recorded field notes, and mapped patterns of vegetation across 35 percent of the state, about 155,000 km^2 (Colwell 1977). Lands mapped were predominantly USFS lands, but extensive tracks of private land, and three national parks (Lassen, Yosemite, and Sequoia/Kings Canyon), were also included (Griffin and Critchfield 1972, Wieslander 1985). The project also collected 25,000 plant voucher specimens, which are housed at the Jepson Herbarium, University of California, Berkeley. These data

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[2] Ph.D., Department of Environmental Science and Policy, University of California, Davis, CA 95616. email: jhthorne@ucdavis.edu.

[3] Analyst, Information Center for the Environment, Department of Environmental Science and Policy, University of California, Davis, CA 95616. e-mail: jhonig@ucdavis.edu.

[4] GIS Specialist, Information Center for the Environment, Department of Environmental Science and Policy, University of California, Davis, CA 95616. e-mail: slthrasher@ucdavis.edu.

[5] Programmer, Information Center for the Environment, Department of Environmental Science and Policy, University of California, Davis, CA 95616.

[6] Graduate Student, Animal Behavior Graduate Group, University of California, Davis, CA 95616. e-mail: trkelsey@ucdavis.edu

[7] Staff, Department of Landscape Architecture, University of California, Davis, CA 95616. e-mail: bjmorgan@ucdavis.edu.

collections are an important vegetation legacy; and all components except the vegetation maps have been digitized for preservation and are available for statewide analyses (Ertter 2000; Kelly and others 2005; plot data are available at http://vtm.berkeley.edu; photographs are available at http://www.lib.berkeley.edu/BIOS/vtm/). The vegetation maps for the central and northern Sierra Nevada have been digitized, and an effort to complete the digitization of these materials is underway (Thorne and others in press; http://cain.nbii.org/plants_animals/plants/wieslander).

The VTM project provided the foundation for much of the current knowledge of vegetation in California. Published biogeographic works include elevational transect maps of vegetation (Critchfield 1971), the distribution of California’s trees (Griffin and Critchfield 1972), and the distribution of range brushlands and shrubs (Sampson and Jespersen 1963). The vegetation plot data have been used in numerous studies, including community classifications (Allen and others 1991, Allen-Diaz and Holzman 1991, Jensen 1947), and vegetation change (Bouldin 1999, Bradbury 1974, Franklin and others 2004, Minnich and Dezzani 1998, Minnich and others 1995, Taylor 2000, Taylor 2004a, b). Wieslander originally intended that the plots and vegetation maps be used together to determine extent and composition of vegetation (Wieslander 1985, Colwell 1977). This report represents an initial effort in that regard, for a limited area and theme. A number of early works also used parts of the VTM collection (Weeks and others 1934, 1943, Wieslander and Jensen 1946).

We developed GIS-compatible versions of the VTM maps for 30,236 km^2 in the central Sierra Nevada. Since individual species were recorded by polygon, we queried the digital maps for the distributions of the five important oak tree species in the region: *Quercus chrysolepis, Q. douglasii, Q. kelloggii, Q. lobata,* and *Q. wislizenii.* The VTM maps also contain information on vegetation seral condition by polygon, included in summaries presented here. We developed summary information for four *Quercus* shrub species in the region: *Q. berberidifolia, Q. durata, Q. garryana var. breweri,* and *Q. vaccinifolia.* Using VTM vegetation plot data, we examined the distribution of size classes determined by the diameter at breast height (DBH) for *Quercus* tree species for the plots in our study region. Finally, we compared the extents of some tree species with modern extents of vegetation types that contain them by using CalVeg, a map produced by the USFS in 1996 (Schwind and Gordon 2001). CalVeg did not cover the entire study area, so change was measured for the area of overlap between the maps, comprising 16,978 km^2, much of which was above the general elevation of oak tree distributions.

Methods

Development of GIS-compatible versions of the historic maps was an involved process, detailed elsewhere (Thorne and others in press). Generally the steps, in order, were: 1) scanning the original maps at 300 dots per inch; 2) scanning identical editions of the United States Geological Survey topographic maps as those the VTM vegetation maps were drawn on; 3) geo-rectifying the USGS topographic maps; and 4) registering the VTM vegetation maps onto them. Once a VTM vegetation map was geo-referenced, it could then be 5) traced using an on-screen digitizing technique that combined ArcInfo GIS software (ESRI 2006) with a WaCom tablet and digital pen (WaCom 2004). When the polygons were completed, they were 6) attributed with species codes written on the original VTM vegetation maps for each polygon. These species codes were used to 7) assign species names, using the Jepson Manual (Hickman 1993) naming conventions. Each polygon could then be 8) represented by an aggregate string of dominant plant species that each occupied at least 20 percent of the polygon's area. Finally, we 9) assigned the species aggregations to California Wildlife Habitat Relationship (CWHR) Models (California Department of Fish and Game 2004), which are habitat descriptors, using a combination of species and seral information.

We generated species-level queries to identify polygons that held any of the species of *Quercus* in them. We identified the *Quercus* position in the species string as follows: If the species was positioned first, we classed it the most dominant; if it occurred in 2nd or 3rd position, it was assumed less prevalent; and if it occurred after (4th-6th position), it was assumed still less dominant, relative to the species listed before it. Once the polygons containing each *Quercus* species were identified, they were used for summary and map production purposes (*table 1*, *figs. 1*-*6*). VTM crews recorded when a polygon's vegetative cover was low, due to either recent burning or recent logging. We incorporated these values to determine how much of each species' extent was in early seral condition. Using the CWHR classes we derived, we were able to assess the percent of each tree species that was resprouting and was in a chaparral condition. We counted the number of polygons each species occupied.

Finally, we derived an elevation distribution by sampling a digital elevation map using the centroid of each polygon. We used a 30-m digital elevation model that had been smoothed to a 250-m cell size using the focal mean command (ESRI 2006). The coarser resolution was used because a preliminary effort to register topography underlying the Placerville quadrangle VTM vegetation map to a modern digital topographic map surveyed using aerial images indicated spatial inaccuracies of up to 270 m, although in many places the error is lower. This level of spatial error is slightly higher than that found by Kelley and others (2005) in their study of the VTM plots. Since we wanted an average elevation for each polygon, we reasoned that resampling the elevation map was an appropriate way to smooth the elevations and obtain a reasonably accurate estimate of elevation.

We downloaded the VTM vegetation plot data files from the UC Berkeley Web site, combined the geographic file with two species files provided, and built queries to select all plots that had species of the genus *Quercus* in them. This subset of plots was then reduced to those plots in our study region. We characterized the general size distribution and height class for oaks species using the plot data. Percent of each species in each DBH size class was multiplied by the area occupied by each species in polygons to derive a landscape estimate of the area in different size classes. We felt this approach was valid because of the high number (> 200) of plots containing most species, and the fact that the VTM crews sampled vegetation with plots to represent the condition of that vegetation on the landscape (Wieslander field methods unpublished). Subsequently, we intersected the plots with *Quercus*-occupied polygons in a GIS, using a 20-m buffer. We recorded the proportion of plots to polygons for each species, examined congruence between species recorded in plots and those recorded in polygons, and determined the percent of plots that occurred in polygons with matching *Quercus* species. We compared elevation distributions obtained from the polygons with those obtained from plots for each tree species.

We compared the total extent of different *Quercus*-containing CWHR types between the VTM and the CalVeg map. Because of the spatial accuracy issues with the older data, we did not intersect those maps to show where change had occurred.

The tabular comparison permits a sense of the magnitude of change, and was only possible for oak species that were identifiable in the CWHR classes, a subset of all the species originally mapped.

Results

1. VTM Map Summaries

Oak species were found on 7,744 km^2 of the study region, in 14,941 polygons (*table 1*). Of that terrain, 21.7 percent (1,683 km^2) and 9 percent (697 km^2) were in early seral condition due to recent fires or logging, respectively. We measured the proportion of each tree species estimated to be resprouting, and in shrub form, by compiling the CWHR chaparral classes developed for each polygon (*table 1*). *Q. kelloggii, Q. lobata,* and *Q. douglasii* had less than 10 percent of their area in chaparral types, while the resprouting shrub form of *Q. wislizenii* was 25 percent. For tree species, most of the recently burned area was classed as chaparral (67 to 89 percent). The same was true for shrubs, excepting *Q. vaccinifolia*, which grows at higher elevation, and was classed as a chaparral type only 54 percent of the time, and for which only 25 percent of the area burned was classed as chaparral.

Q. douglasii was the most widely distributed tree, covering 3,132 km^2. *Q. garryana* was identified in only two polygons, and is excluded from map summaries. We present maps for six species containing enough extent to map (*figs. 1-6*), and report the elevation distribution of each species by quartile (*table 1*).

2. VTM Plot Summaries

There were 5,276 VTM vegetation plots in the study area, of which 1,628 contained species in the genus *Quercus* (*fig. 7, table 2*). Shrubs were generally not well sampled by the plot data, with only *Q. vaccinifolia* providing enough samples to be useful in generalizing to landscapes. There were no plot records for *Q. berberidifolia*, four for *Q. durata*, and 19 for *Q. garryana breweri*; these species were excluded. Of each tree species, between 64 and 84 percent were in the smallest DBH class, while 10 percent of *Q. lobata* was in the largest class, more than 91 cm DBH. From 5 to 25 percent of all tree species were in the second size class (*table 2*).

The overall elevation distribution of *Quercus* in VTM plots ranged from 7 to 2,865 m. We broke this distribution into quartiles and identified the percent plots in each class for each species (*table 2*). *Q. wislizenii* had the broadest elevation distribution, with 49 percent in the lowest elevation but 18 percent in the highest. *Q. chrysolepis* also had a broad elevation distribution, extending upslope with 31 percent in the highest elevation class. Tree height was relatively evenly distributed among height classes, with the exception of *Q. lobata*, which had few trees in the middle categories.

3. Combined Map/Plot Summaries

The most heavily sampled tree was *Q. kelloggii*, which was recorded in a plot for every 305 ha of terrain that VTM vegetation maps showed as having black oak. *Q. vaccinifolia* had a sampling ratio of one plot per 261 ha *(table 3*). *Q. douglasii* had the lowest sampling ratio, appearing in plots once for every 685 ha.

We classed each species' elevation distribution as measured by polygon centroids into the elevation quartiles defined from the VTM plot data. Comparison of elevation distributions derived from the plot and polygon data independently showed good agreement between the two data sources (*table 3*). *Q. wislizenii* is the only species that showed a difference; with 18 percent shown in the highest elevation break as measured by polygons, and only 0.8 percent registered in the plot data. The general registration of plots into polygons was tested by examining the proportion of plots whose *Quercus* species were also identified in the polygon it occupied. Only two of the five tree species had more than 50 percent of the plots correct by this measure. We therefore did not do further work with the plot/polygon combined files.

4. VTM Comparison to Modern Map Summaries by Table

Twenty-three CWHR habitat types in the CalVeg map were associated with *Quercus* species. We reduced these to 11 classes each containing a unique combination of potential *Quercus* species, for which we could calculate changes in extent (*table 4*). These changes do not represent all changes on the landscape (Thorne and others in press). *Q. douglasii* is a measurable species, and has lost 837 km^2 of extent in the region, predominantly replaced by California annual grasslands. *Q. kelloggii* occurs in many habitat types. In its association as a subdominant under conifers, it lost 1,493 km^2 (25 percent of its range). However, while the dominant overstory appears to have been lost, *Q. kelloggii* appears to have maintained extent via gains in montane hardwood and montane hardwood-conifer. These gains may also have been beneficial for *Q. chrysolepis* and *wislizenii*. Changes under 100 km^2 are probably below the resolution of both the maps and the taxonomic classification to identify, so positive change identified for *Q. lobata* is likely an error, associated with the finer mapping scale of CalVeg, which could identify much smaller stands.

Discussion

The most dominant trends measured were the decline of *Q. douglasii*, being replaced by annual grasslands, and the loss of coniferous ecosystems in which *Q. kelloggii* was a dominant understory species. The loss of 837 km^2 of *Q. douglasii*, and gain of 1,077 km^2 of California annual grasslands led to the conclusion that grasslands were the predominant landcover type to which blue oak woodlands have been converted. More detailed accounting of the changes in landcover extents by quad in the study area is in Thorne and others (in press). *Q. kelloggii* does not appear to have lost spatial extent in the conversion, but it now is represented in more polygons of montane hardwood and montane hardwood-conifer. It also appears that habitat types in which *Q. vaccinifolia* is found have been greatly reduced. Whether this has led to a decrease in this species is not clear. Changes in extent under 200 km^2 (less than 1.2 percent of the area compared for historic trends) may represent differences in mapping systems used, rather than actual change. Particularly, *Q. lobata* was indicated to have increased, while it is generally thought to be greatly reduced due to anthropogenic disturbance. Our result is likely due to the finer spatial resolution at which the modern CalVeg was mapped (1 ha minimum mapping unit, derived from 30 m satellite imagery). The finer imagery permitted the identification of smaller groups of trees, increasing the overall extent for that species.

The VTM plot data were geo-registered using a different approach than the VTM vegetation map data. The plot data were geo-registered onto historic digital topographic maps, which had already been rectified to modern imagery. The historic vegetation maps were registered to scanned 1930s versions of topographic maps, which had not been registered to modern map scans. We found that the old maps have random spatial errors of up to 270 m. We suspect that the differing registration techniques led to the poor matching of species between plot and polygon when we tried to combine them. This indicates a need for another round of processing on the VTM vegetation maps to bring them into alignment with modern topographic maps. Once that has been accomplished, it will likely result in much higher concurrence between plot and polygon species lists. The VTM mappers would survey both polygon and plot at the same time, with the objective that the plot be situated in vegetation characteristic of the polygon they had delineated (Wieslander 1985). Therefore, it is likely that many of the plots occur along the perimeters of polygons, and while they likely all described their respective polygons at the time, the differing registration techniques used made initial comparisons in GIS non-informative.

The VTM field manual recommends sampling vegetation with plots, “as often as is necessary to obtain a true picture of conditions for each vegetation type” (Wieslander unpublished), which we interpreted to mean that the data in the plots was representative of conditions by vegetation type as a whole on the landscape. The landscape sampling effort represented by both VTM plots and vegetation maps is considerable, and permitted some unification of the data without having to be spatially explicit. For example, *Q. kelloggii* appeared in VTM plot records once for every 2.5 km^2 of terrain it occupies in the VTM vegetation maps of our study area, representing 941 sample points on 2,346 km^2. All tree species, excepting *Q. lobata*, and *Q vaccinifolia,* were represented more than 200 times in the plot data (points to area mapped in *table 3*). The distribution of size classes by species in the plot data is therefore likely representative of the entire distribution of size classes by species, so we felt confident in multiplying the spatial extent of the species by the size classes to get an estimate of the proportion of landscapes in different size classes.

Elevation distribution was measured by both the polygon and the plot distributions. The distributions closely agreed, a form of validation for the historic data. An interesting question is the definition of the elevation zone within which the majority of each species occurred; narrower distributions, as seen in blue and valley oak, may be susceptible to climate change perturbations.

The VTM data permit a detailed view of the historical landscapes of California. Spatial extent, stand structure, and elevation distributions of individual species were calculated, and can be used in future landscape change analyses. Taxonomic detail in the historic data was high and spatial accuracy was moderate, with horizontal error of up to 270 m. However, when looking at landscape-level dynamics, and when reviewing tabular summaries, rather than intersected maps, trends emerged that likely reflect actual change in the central Sierra Nevada.

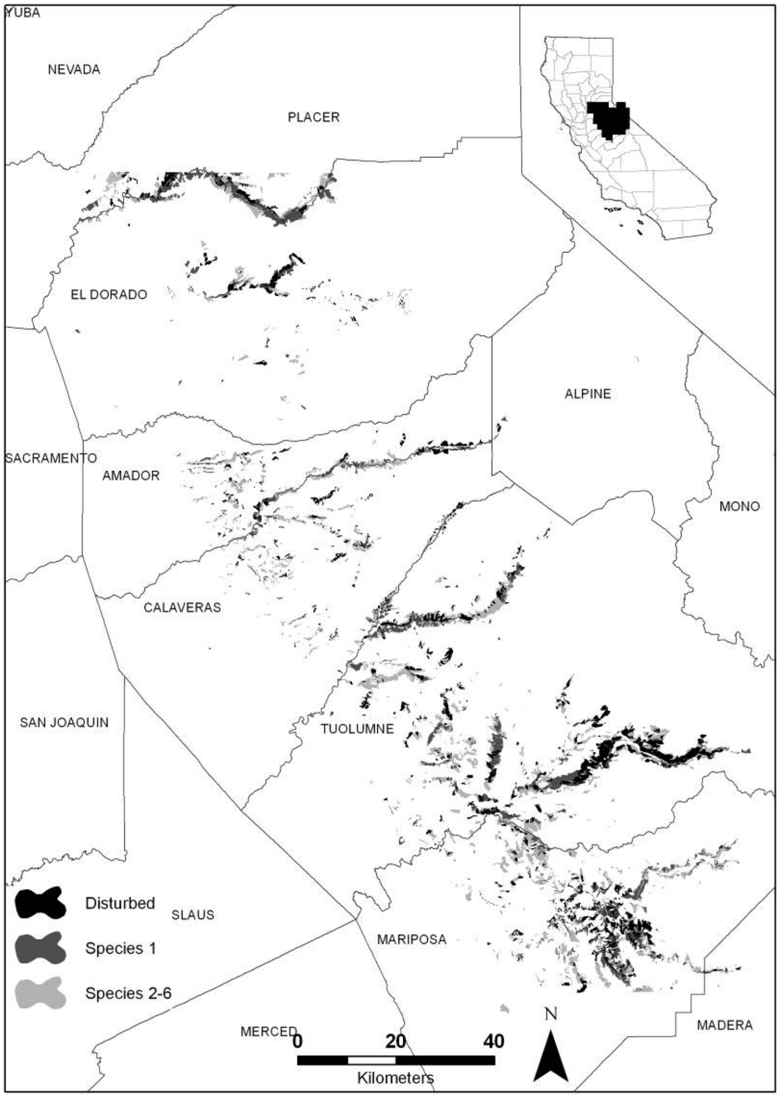

Figure 1—*Quercus chrysolepis*, the 1930s distribution of canyon live oak in the central Sierra Nevada. The species number indicates at what point the oak was recorded in the order of species listed per polygon. The less dominant species classes (species 2-3 and species 4-6) were combined for visual clarity.

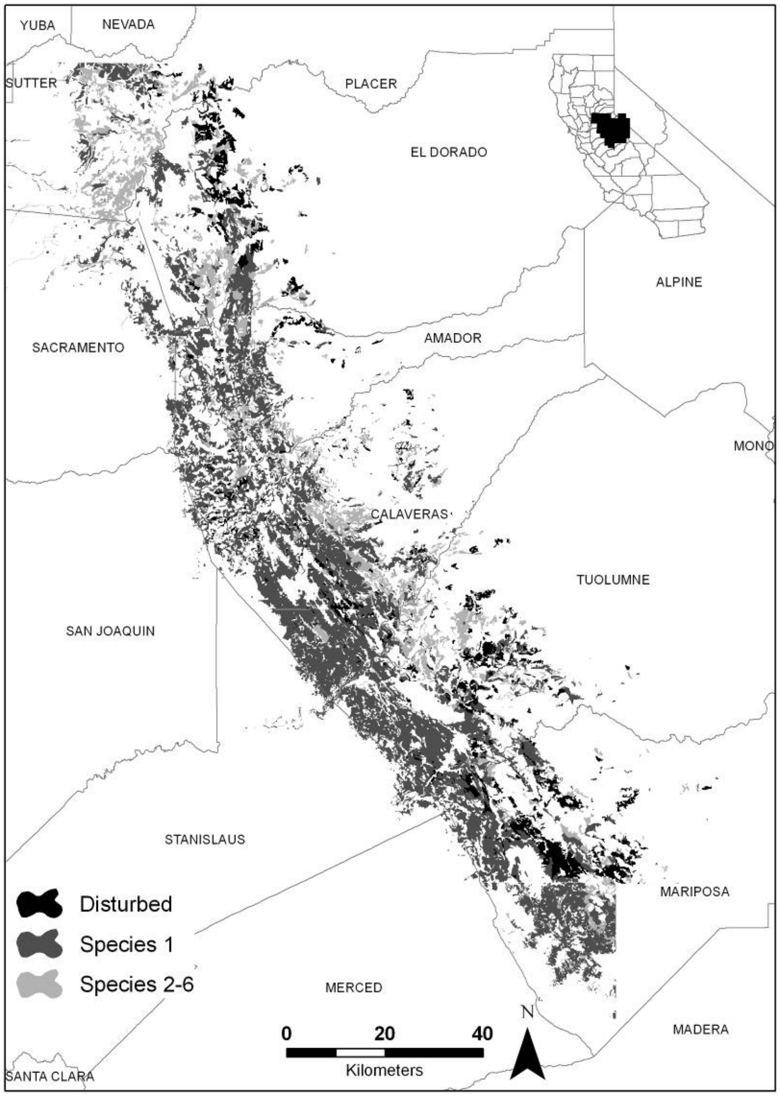

Figure 2—*Quercus douglasii*, the 1930s distribution of blue oak in the central Sierra Nevada. The species number indicates at what point the oak was recorded in the order of species listed per polygon. The less dominant species classes (species 2-3 and species 4-6) were combined for visual clarity.

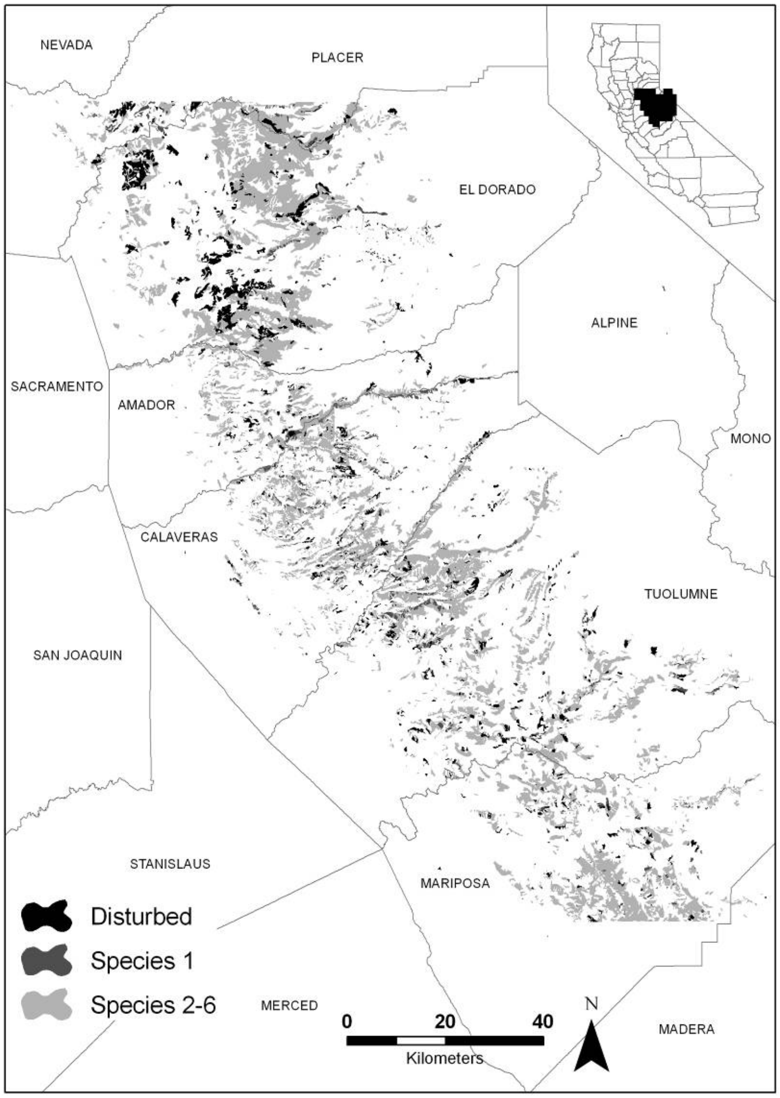

Figure 3—*Quercus kelloggii*, the 1930s distribution of black oak in the central Sierra Nevada. The species number indicates at what point the oak was recorded in the order of species listed per polygon. The less dominant species classes (species 2-3 and species 4-6) were combined for visual clarity.

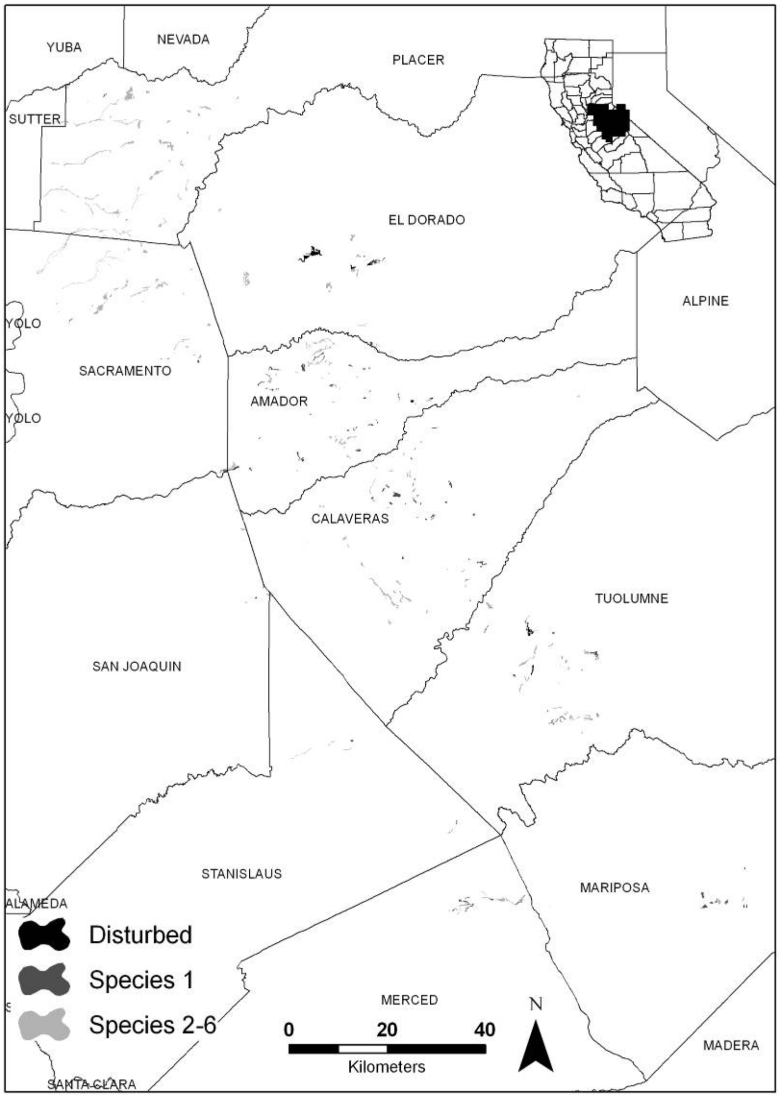

Figure 4—*Quercus lobata*, the 1930s distribution of valley oak in the central Sierra Nevada. The species number indicates at what point the oak was recorded in the order of species listed per polygon. The less dominant species classes (species 2-3 and species 4-6) were combined for visual clarity.

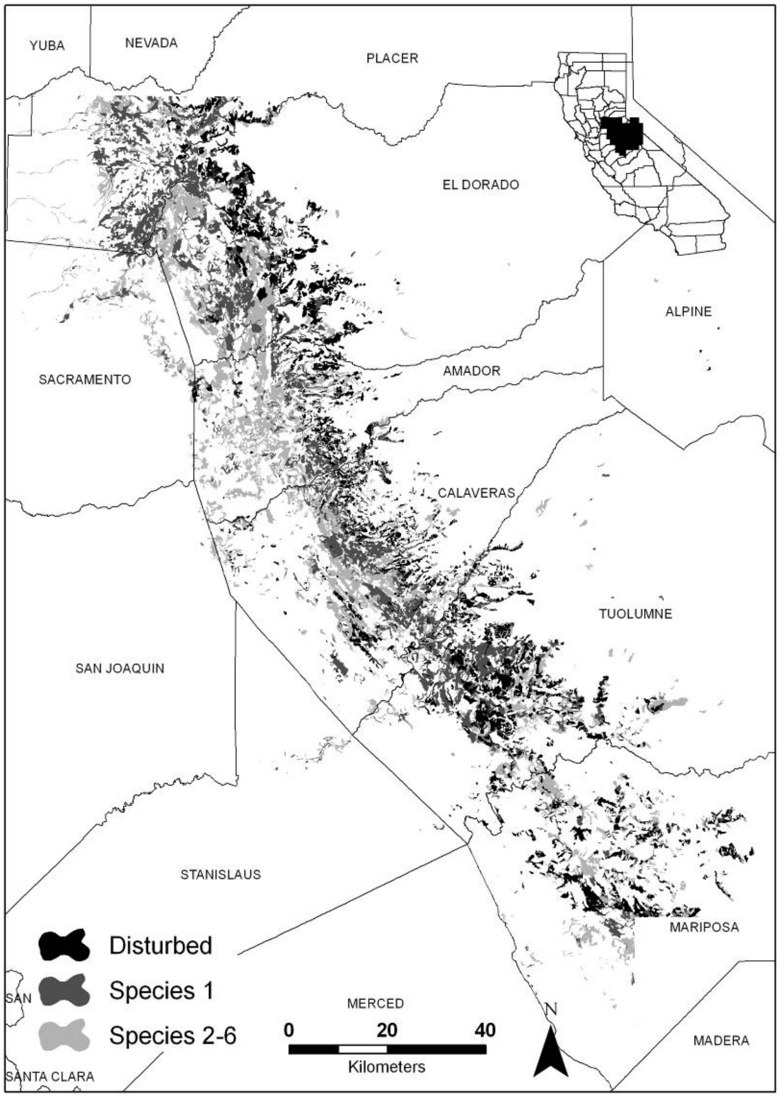

Figure 5—*Quercus wislizenii*, the 1930s distribution of interior live oak in the central Sierra Nevada. The species number indicates at what point the oak was recorded in the order of species listed per polygon. The less dominant species classes (species 2-3 and species 4-6) were combined for visual clarity.

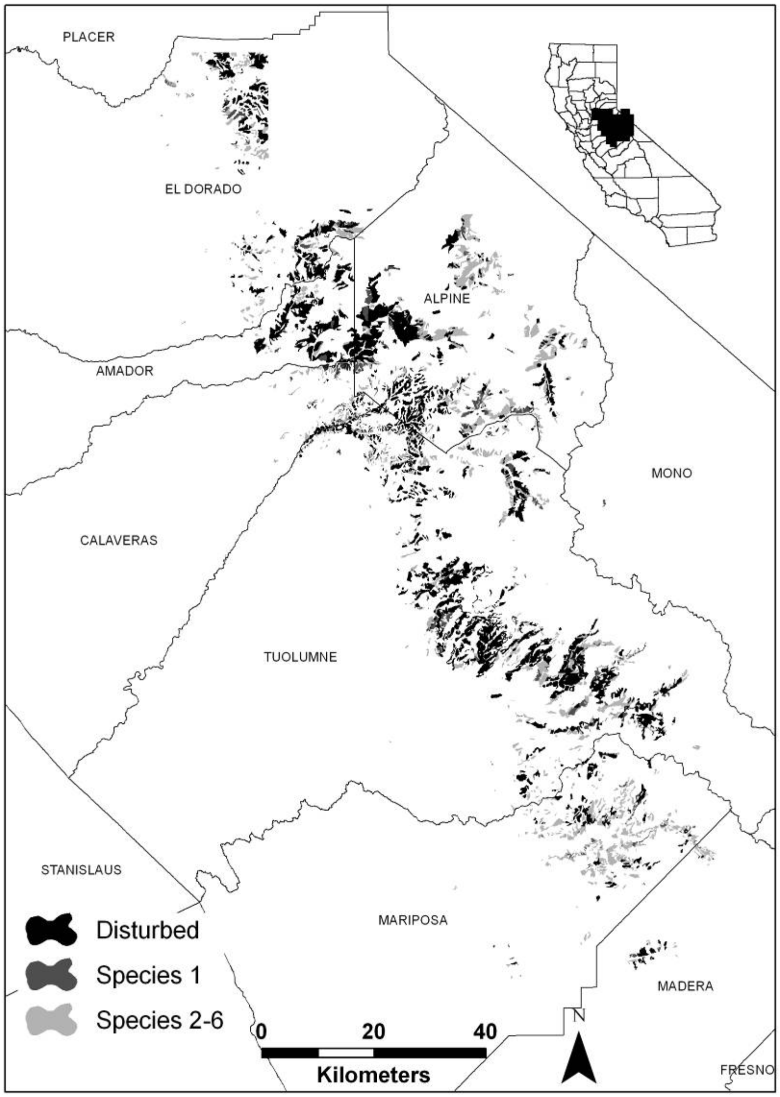

Figure 6—*Quercus vaccinifolia*, the 1930s distribution of Huckleberry oak in the central Sierra Nevada. The species number indicates at what point the oak was recorded in the order of species listed per polygon. The less dominant species classes (species 2-3 and species 4-6) were combined for visual clarity.

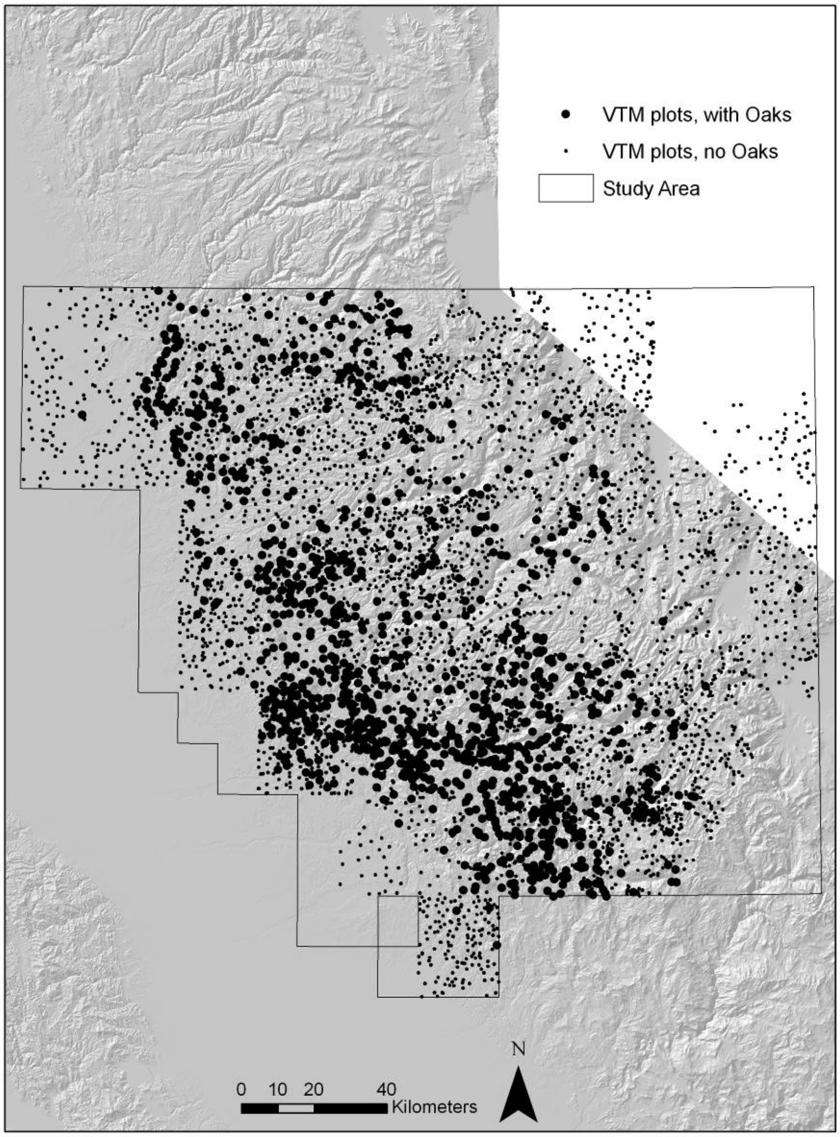

Figure 7—The distribution of 5,276 VTM vegetation plots in the central Sierra Nevada. The 1,628 plots with species in the genus *Quercus* are shown larger than those without.

Table 1—*Area extents for nine* Quercus *species in the central Sierra Nevada. The area occupied by the species in a chaparral Wildlife Habitat Relationship Type (either Mixed Chaparral or Montane Chaparral) is shown after the total extent of the type. The area of the species recently burned or logged is shown, followed by the area in which the species was listed first in the string of species; second or third; and higher; which represent different levels of prevalence by the species as compared to others it occurs with.*

Species	***Quercus chrysolepis***	***Quercus douglasii***	***Quercus kelloggii***	***Quercus lobata***	***Quercus wislizenii***	***Quercus berberdifolia***	***Quercus durata***	***Quercus vaccinifolia***	***Quercus garryana breweri***
Total Area (ha)	101,795	313,207	234,465	8,945	279,250	930	**1,647**	**100,237**	**1,613**
Chaparral Area (ha)	16,656	27,705	23,372	417	67,619	902	1,202	25,132	1,293
Total Area Burned	21,670	41,539	27,022	596	75,788	189	489	466	547
Total Area Logged	8,695	469	4,002	8	505	0	30	56,067	0
Species Listed First (ha)	46,459	225,318	21,602	2,375	142,537	242	1,017	18,853	681
Number of Polygons (SP1)	1,379	2,473	925	137	3,265	9	19	512	55
Species Listed Second or Third (ha)	47,610	86,260	190,906	5,783	131,418	666	531	65,701	710
Number of polygons (SP2_3)	1,312	1,336	3,429	189	2,305	14	7	1,620	36
Species listed 4th, 5th, or 6th (ha)	7,726	1,628	21,958	786	5,295	23	99	15,683	222
Number of polygons (SP4_5_ 6)	173	26	308	21	124	1	2	296	3
Total Number of polygons	2,864	3,835	4,662	347	5,694	24	28	2,428	94
Elevation Range (m)	548	342	622	591	330	213	185	377	215
Percent of Species Extent in Chaparral	16	9	10	5	24	97	73	25	80

Table 2— *Summary of VTM plot data for six species of* Quercus *in the central Sierra Nevada.*

Species	***Quercus chrysolepis***	***Quercus douglasii***	***Quercus kelloggii***	***Quercus lobata***	***Quercus wislizenii***	***Quercus vaccinifolia***
Number of Plots	215	457	941	44	534	261
Elevation 7- 457m (%)	3	65	6	47	50	0
Elevation 457 - 823 m (%)	25	26	20	47	27	0
Elevation 823 - 1295 m (%)	41	10	33	7	6	0
Elevation > 1295 m (%)	31	0	40	0	18	100
Diameter Class 4 – 11” (%)	83	83	67	65	80	
Diameter Class 12 – 23” (%)	6	15	26	26	12	
Diameter Class 24 – 35” (%)	4	2	6	0	7	
Diameter Class > 36” (%)	1	0	1	10	1	
Height Class 0 - 4.5 m (%)	25	17	27	73	30	100
Height Class 4.5 - 7.6 m (%)	30	46	21	0	20	
Height Class 7.6 - 10.7 m (%)	20	30	26	7	16	
Height Class > 10.7 m (%)	25	5	25	20	33	

Table 3— *Combination of historic VTM vegetation maps and VTM plot data for the Central Sierra Nevada.*

Species	***Quercus chrysolepis***	***Quercus douglasii***	***Quercus kelloggii***	***Quercus lobata***	***Quercus wislizenii***	***Quercus vaccinifolia***
Number of Plots	215	457	941	44	534	261
Ratio of Area Occupied by Species per VTM Plot with species (ha)	473	685	249	203	520	384
Number of plots correctly classed	84	344	389	2	333	
Number of plots incorrectly classed	131	113	552	42	201	
Percent Plots correctly classed	39	75	41	5	62	
Area Occupied by Each Diameter Size Class (ha)						
Diameter Class 4 – 11”	84,900	260,082	158,122	5,771	222,746	
Diameter Class 12 – 23”	5,733	4,158	6,000	108	8,183	
Diameter Class 24 – 35”	723	3	37	0	23	
Diameter Class > 36”	5	1	13	37	7	
Percent Plots by Elevation Quartile						
Elevation 7- 457m (%)	3	65	6	47	50	0
Elevation 457 - 823 m (%)	25	26	20	47	27	0
Elevation 823 - 1295 m (%)	41	10	33	7	6	0
Elevation > 1295 m (%)	31	0	40	0	18	100
Percent Polygons by Elevation Quartile						
Elevation 7- 457m (%)	4	65	9	59	43	0
Elevation 457 - 823 m (%)	25	28	32	31	45	0
Elevation 823 - 1295 m (%)	44	7	36	9	12	0
Elevation > 1295 m (%)	27	0	24	0	1	100
Number of Polygons by Elevation Quartile						
Elevation 7- 457m (#)	115	2,481	421	205	2,439	0
Elevation 457 - 823 m (#)	712	1,092	1,474	109	2,549	2
Elevation 823 - 1295 m (#)	1,260	263	1,663	32	660	6
Elevation > 1295 m (#)	776	0	1,103	1	48	2,418

Table 4— *Measure of change in* Quercus *occupied California Wildlife Habitat Relationship (CWHR) types between 1934 and 1996 in the central Sierra Nevada. Species that occur in the CWHR class are shown in parentheses*.

CWHR Classes	**VTM (ha)**	**CalVeg (ha)**	**Area Gained or Lost (ha)**
Montane Hardwood (*Q. kelloggii, chrysolepis, wislizenii*)	112,336	223,119	110,783
Annual Grassland (AGS)	180,202	287,920	107,718
Montane Hardwood-Conifer (*Q. kelloggii, chrysolepis, wislizenii*)	31,962	97,057	65,095
Mixed Chaparral (*Q. kelloggii, chrysopelis, wislizenii, durata, berberdifolia, garryana breweri*)	66,241	77,280	11,039
Douglas Fir (*Q. kelloggii, chrysolepis*)	32,122	42,046	9,924
Valley Oak Woodland & Riparian (*Q lobata, douglasii*)	2,858	3,171	313
Aspen, Eastside Pine, Subalpine Conifer, Lodgepole Pine, Red Fir (*Q vaccinifolia*)	148,096	123,006	-25,090
Montane Chaparral (*Q kelloggii, vaccinifolia, durata, berberdifolia*)	71,990	41,404	-30,586
Chamise-Redshank Chaparral (*Q durata, berberdifolia, kelloggii*)	77,387	33,243	-44,144
Blue Oak Woodland, Blue Oak Foothill Pine (*Q douglasii*)	242,208	158,460	-83,748
Ponderosa Pine, Sierran Mixed Conifer, White Fir, Jeffery Pine Montane Riparian (*Q kelloggii*)	593,983	444,603	-149,380

Acknowledgements

This paper is dedicated to Dr. Paul Zinke, professor at UC Berkeley who recently passed away, and who worked on the Wieslander Vegetation Type Map project when a graduate student. I had the honor of meeting him at his house and listened to him recall moments from those times. Funding for this project was provided by Public Interest Energy Research (PIER grant # 500-02-004) and by a grant provided by the United States Forest Service, Pacific Northwest Research Station. Lab space was provided by Dr. Jim Quinn, University of California, Davis, Department of Environmental Science and Policy.

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Continue

Monitoring Understory Composition of Blue Oak Woodlands on Conservation Easements[1]

Adena R. Rissman,[2] Sarah E. Reed,[2] Chuck Hughes,[3] and Richard Reiner[4]

Abstract

Conservation easements are an increasingly popular strategy for conserving biological diversity on private land. Long-term vegetation monitoring on conservation easements can provide critical information on persistence of biological diversity and abundance of invasive species. We sampled understory plant composition on five of The Nature Conservancy's conservation easements in the Mt. Lassen foothills of Northern California. We established 73 plots of 10-meter radius, measured species composition with the point-intercept method, and compiled a full species list for each plot in 2005 and 2006. We found significant differences in the relative cover of native and non-native annual grasses and annual forbs among easement properties. Relative cover of native plants was significantly higher in herbaceous plots (50 percent) than in plots with blue oak (*Quercus douglasii*) canopy (21 percent). We found medusahead (*Taeniatherum caput-medusae*) in 64 percent of plots and yellow star thistle (*Centaurea solstitialis*) in 9 percent of plots. Overlap of species composition between years was correlated with difference in date sampled each year but not correlated with confidence in plot relocation. Our analysis of community diversity and relative abundance provides a baseline for future change. Finally, we make recommendations for the design of future monitoring efforts on conservation easements.

Keywords: Biological monitoring, conservation easements, Lassen foothills, plant diversity, point-intercept, Quercus douglasii.

Introduction

Conservation easements are an increasingly popular tool for conserving private land in the United States (Merenlender and others 2004). Conservation easements are voluntary agreements between private landowners and a land trust or government agency to restrict land use in exchange for payment or tax reductions (Byers and Ponte 2005, Gustanski and Squires 2000). Conservation easements are also used as mitigation for development. California oak woodlands are more than 80 percent privately owned (Pavlik and others 1991), and conservation easements are an important tool for conserving biodiversity and working ranches on California oak woodlands (Sulak and others 2004). Recent scrutiny of conservation easement transactions (Reiterman 2005, Stephens and Ottaway 2003) has led to calls for

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[2] Ph.D. Student, Department of Environmental Science, Policy, and Management, 137 Mulford Hall, University of California, Berkeley, CA 94720. e-mail: arissman@nature.berkeley.edu, sreed@nature.berkeley.edu

[3] Botanist, Sycamore Environmental Consultants Inc., 6355 Riverside Blvd Ste. C, Sacramento, CA 95831. e-mail: cchughes@pacific.net

[4] Ecologist, The Nature Conservancy, 500 Main St. Chico, CA 95928. e-mail: rreiner@tnc.org

additional monitoring on conservation easement properties (Kiesecker and others 2007, Rissman and others 2007a). Monitoring of easements can be divided into two general activities: compliance monitoring and ecological monitoring beyond compliance (Rissman and others 2007b). Compliance monitoring requires easement holders such as land trusts to periodically return to a property to assess whether the terms of the easement agreement are being upheld by the landowner. Ecological monitoring, the focus of this paper, differs from compliance monitoring in that it collects data on species and natural communities to provide assurance that easement agreements are effective in meeting conservation goals beyond the specific terms of the easement. Monitoring species composition alone cannot identify the drivers of vegetation change but can help assess whether diversity is retained on the easements over the long-term.

The Nature Conservancy acquired conservation easements on more than 71,000 acres in the Mt. Lassen foothills in Northern California to conserve blue oak woodlands and other conservation targets (The Nature Conservancy 2006). Because biodiversity protection is one of the primary goals of the Lassen foothills project, ecological monitoring is valuable for providing information on the status and trends of biodiversity elements in blue oak (*Quercus douglasii*) woodlands (Reiner and others 2001). We undertook an easement monitoring project to document the status of understory plant communities, avian communities, and oak woodland canopy structure, and to map the vegetation communities of the easements. In this paper, we focus on understory vegetation monitoring of blue oak woodlands and interspersed grasslands on the conservation easements. Two of the primary threats to the long-term persistence of blue oak woodlands are non-native plant invasion and poor oak recruitment (Pavlik and others 1991), and our focus on understory composition addresses both of these factors.

Understory vegetation is a common choice for monitoring because plants are generally sedentary and relatively easy to monitor, sensitive to site-specific variation (Spellerberg 2005) and because vegetation composition surveys can provide important information on common and rare native and invasive species. The vegetative understory of California oak woodlands is dominated by non-native annual grasses and forbs (Jimerson and Carothers 2002, Pavlik and others 1991). Unusual or poor soils and rock outcroppings can provide native species refuge from highly competitive invasive species (Anderson and others 1999). Portions of the Lassen foothills have thin, volcanic soils and exposed bedrock that supply habitat for native species with limited distributions.

Our primary objective was to characterize the understory vegetation of five conservation easements in the Lassen foothills region. Specifically, we compared indices of species diversity, native and non-native functional guilds, abundance of two invasive species medusahead (*Taeniatherum caput-medusae*) and yellow star thistle (*Centaurea solstitialis*), and presence of blue oak seedlings among easement properties. A comparison across easements can provide a greater understanding of the relative contribution of each property to protecting native plant diversity and help set priorities for land management including invasive species control. Next, we determined some of the site and landscape-scale factors that predict community composition. Finally, we assessed sampling error and used this information to provide recommendations for monitoring strategies for detecting patterns in species composition and change over time.

Study Area and Methods

Study Area

The study was conducted on five ranches in eastern Tehama and Shasta Counties, California. All of the ranches are within The Nature Conservancy's Lassen foothills project area, which was established in 1997 to protect the region's under-protected or rare species and natural communities. Among these conservation targets is a large and ecologically intact blue oak woodland landscape. Blue oak is endemic to California, occurs mostly on private lands, and is threatened by residential development and woodcutting in many parts of its range (Pavlik and others 1991). The Nature Conservancy's primary conservation strategy in the area is the purchase of conservation easements. These easements restrict development, woodcutting, and other extractive uses and allow the properties to be maintained as privately owned cattle ranches.

Blue oak woodlands in the Lassen foothills project area cover approximately 300,000 acres and range from dense stands to open savannahs. Scattered grey pine (*Pinus sabiniana*), California buckeye (*Aesculus californica*), and shrubs such as buckbrush (*Ceanothus cuneatus*) are interspersed. The understory is composed primarily of annual grasses and forbs.

The ranches sampled in this study are situated between 500 and 1,500 feet in elevation and vary from 1,000 to 10,000 acres in size. Each ranch was managed for livestock production with similar stocking rates and a long history of cattle grazing. January through May rainfall totaled 17 inches in 2005, and 26 inches in 2006 (California Climate Data Archive 2006). The soils originated from the volcanic Tuscan Formation laid down two to four million years ago over volcanic flows and older marine sediments. The Tuscan Formation is younger than much of the northern Sierra foothills and therefore has thinner soils and more exposed bedrock (California State University, Chico).

Study Design

We established 73 plots of 10-meter radius (314 m^2), locating between 12 and 24 plots on each of five recent conservation easement properties in 2005. In 2006 we added four plots for a total of 77 plots in that year, which included 61 blue oak-dominated plots and 14 herbaceous-dominated plots. Plots were located a minimum of 200 m apart to allow for avian point count sampling at the same locations, and to sample within large portions of each property. We collected species composition data in April and May of each year using two methods: point-intercepts and a full plot species list (macroplot). We employed the point-intercept method to provide a quantitative measure of relative cover. Each plot contained 81 point-intercept surveys, located every 0.5 meter along two 20-meter transects that bisected the plot in a North-South and East-West direction. We recorded all plants touching the pin and any overstory species above the pin. The full species list was recorded during a systematic search of each plot. Plots were relocated in 2006 using GPS with the addition of plot markers where private landowners provided permission to leave permanent markers. Plant nomenclature follows Hickman (1993).

Statistical Analyses

Analysis of sampling effort and error, species diversity (alpha, beta), and community composition was performed in Microsoft Excel and JMP 6.0 (SAS Institute, Inc. 2005). Nonmetric multidimensional scaling (NMS) was performed in PC-ORD 4.2 (McCune and Grace 2002). All species identified in the point-intercept surveys were added to the macroplot data if they were missing from the macroplot species list due to observer error. For the ordination, plants were lumped by genus when not identifiable to species.

For comparisons of species richness we used data from the macroplot surveys. We calculated Shannon (H) diversity at the plot- and property-level using unique species and their proportions of total detections from the point-intercept survey data. For comparisons of beta diversity, we calculated the Jaccard (C_J) index from point-intercept surveys, assuming that sample effort was equal among plots. We conducted one-way analyses of variance (ANOVA) to test for differences in mean values of diversity indices among properties. When we detected a significant difference among means, we used a Tukey-Kramer honestly significant difference (HSD) test to identify significant differences between pairs of means. However, the Tukey-Kramer HSD test is slightly conservative and may not detect significant pairwise differences even when the ANOVA result is significant (Gotelli and Ellison 2004).

We used data from the point-intercept surveys for all species composition comparisons, including relative proportions of species in different guilds, proportions of native species, and detections of critical invasive species. We compared functional guild composition for blue oak and herbaceous-dominated plots from 2006. The one plot in pasture and one plot in interior live oak (*Quercus wislizenii*) woodland were excluded from this comparative analysis. We estimated the extent and frequency of medusahead and yellow star-thistle invasions and blue oak seedling presence in all plots. To minimize variation due to seasonal detectability of these species, we pooled results from 2005 and 2006. We conducted one-way ANOVAs to test for differences in invasive species among properties, and used a Tukey-Kramer HSD test to identify significant differences between pairs of means. We conducted a nominal logistic regression to compare the probability of blue oak seedling occurrence among properties for the 61 blue oak woodland plots.

We chose NMS as an ordination method to characterize differences in community composition among plots and correlate community composition with environmental variables (McCune and Grace 2002). We used 2006 point-intercept data for 76 plots (one plot was excluded for lack of vegetation composition data). Environmental data were either extracted from a Geographic Information System (elevation and slope were obtained from a 10m digital elevation model in ArcGIS 9.0) or collected at each plot (vegetation type, property name, aspect, and percent cover of total vegetation, herbaceous vegetation, hardwood overstory, conifer overstory, low tree-tall shrub vegetation, low-mid shrub vegetation, rock, and bare ground). Point-intercept data were included as proportion of relative cover for each plot and species detected in fewer than 4 percent of plots were excluded. Environmental variables were relativized by the mean of each variable. We used the “slow and thorough” autopilot settings for NMS in PC-ORD with Sorensen’s distance measure, a random starting configuration, 40 runs with real data, six dimensions in the original model and three in the final model, and 90 iterations for the final solution. The final solution was considered stable for instability values lower than 0.0001.

We evaluated our sampling effort and error using data from both the point-intercept and full-plot species composition surveys. We compared the number of species detected using each sampling method and fit a species accumulation curve to the 2006 point-intercept surveys to estimate the total number of species occurring in each plot. We also compared the species composition for each plot between 2005 and 2006. We then ran a forward stepwise regression to determine whether the proportion of species shared between 2005 and 2006 was predicted by the difference in date sampled each year and by a categorical variable indicating our confidence in returning to the same spatial location both years (the 2006 plot was either within inches of the 2005 plot, within several meters of the 2005 plot, or was located solely based on GPS and therefore within about 10 m of the 2005 plot).

Results

Species Diversity

We detected 43.3 ± 9.2 (mean ± SD) species in each macroplot surveyed in 2005, and 43.3 ± 9.9 (mean ± SD) species in 2006. We did not detect a significant difference in mean species richness among the five easement properties in 2005 ($F_{4,68} = 1.63$, $p = 0.18$). In 2006, we did detect a significant difference in mean species richness among properties ($F_{4,72} = 2.92$, $p < 0.05$). Ranch A (S = 47.1) and Ranch E (S = 38.1) properties had the greatest difference in mean species richness; however, a Tukey-Kramer HSD test did not reveal significant differences between any pairs of means.

We also used the Shannon (H) index to test for differences in species diversity among plots and properties, accounting for both the number and relative dominance of species. Because we did not detect a significant difference in species richness between years, we limited our analysis to data collected in 2006. Shannon (H) diversity values were not significantly different among properties ($F_{4,72} = 0.62$, $p = 0.65$), with a plot value of 2.24 and a property value of 3.03.

Finally, we tested for differences in species turnover among plots on each property, using the Jaccard index (C_J) of beta diversity. Values of the Jaccard index are one when all species are shared among plots, and zero when no species are shared. Jaccard values were significantly different among properties ($F_{4,621} = 16.5$, $p < 0.001$). Plots on Ranch E had significantly greater similarity (Mean(C_J) = 0.35) than the other four properties, while pairs of plots on Ranch C shared significantly fewer species (Mean(C_J) = 0.20) than the other four properties.

Functional Guilds

We assessed community composition by functional guild for native and non-native annual and perennial grasses, annual and perennial forbs, ferns, non-graminoids, and shrubs. Annual forbs and grasses dominated the vegetative cover on all properties (*fig*. 1). Annual forbs were 53 percent and annual grasses were 31 percent of relative cover in 2005, and 48 percent and 36 percent, respectively, in 2006. In 2005, there were no significant differences in the mean proportion of annual forb species among properties ($F_{4,68} = 2.14$, $p = 0.09$), but we did find a significant difference in the mean proportion of annual grasses ($F_{4,68} = 5.94$, $p < 0.001$). Plots on Ranch A had a significantly lower proportion of annual grasses ($P_{AG} = 0.247$) than plots on Ranch E ($P_{AG} = 0.334$), Ranch D ($P_{AG} = 0.325$), or Ranch C ($P_{AG} = 0.322$). In 2006, we found significant differences in the mean proportions of annual forbs ($F_{4,72} = 3.23$, $p < 0.05$) and annual grasses ($F_{4,72} = 11.00$, $p < 0.001$) among properties. Plots on Ranch A had a significantly greater proportion of annual forbs ($P_{AF} = 0.533$) than plots on Ranch E ($P_{AF} = 0.436$). Plots on Ranch A also had a significantly lower proportion of annual grasses ($P_{AG} = 0.265$) than the other four properties.

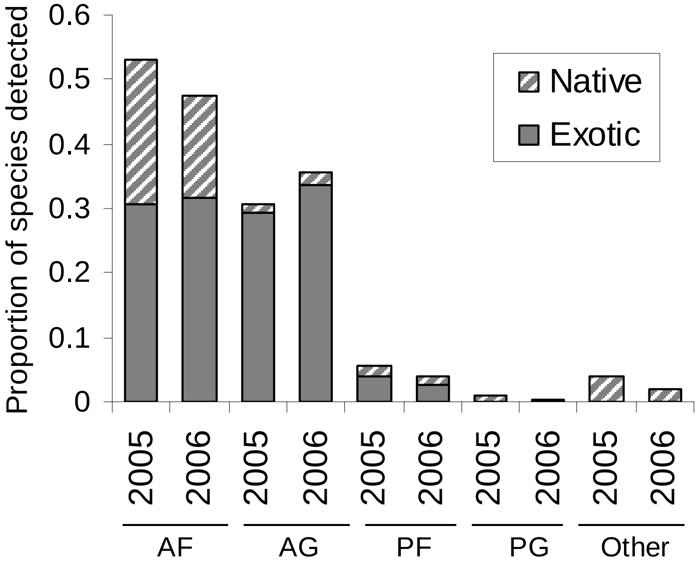

Figure 1—Mean relative cover of different functional guilds, for all properties, in 2005 and 2006 from point-intercept data. Proportions of native and exotic species are indicated for each guild. (AF = annual forb, AG = annual grass, PF = perennial forb, PG = perennial grass, Other = ferns, non-graminoids and shrubs.)

Our surveys indicated that all five properties were substantially invaded by non-native species. Native species comprised 30 percent of cover in 2005 and 22 percent in 2006 (*fig.* 1). In 2005, we detected a significant difference in mean proportions of native species among properties ($F_{4,68} = 4.89$, $p < 0.01$). Plots on Ranch A had a significantly greater proportion of native species ($P_{NATIVE} = 0.387$) than Ranch E ($P_{NATIVE} = 0.235$) and Ranch B ($P_{NATIVE} = 0.226$). In 2006, we did not detect a significant difference in mean proportions of native species among properties ($F_{4,72} = 1.39$, $p = 0.25$), but the rank order of properties was the same as in 2005.

The ten most abundant species made up more than half (59 percent) of relative cover in both 2005 and 2006. Nine of the ten most abundant species each year were in the top ten both years. These were all non-native species: *Bromus hordeaceus, Bromus diandrus, Taeniatherum caput-medusae, Trifolium hirtum, Erodium botrys, Avena barbata, Aira caryophyllea*, *Geranium molle*, and *Trifolium dubium*. While native cover was low, native diversity was high: native species made up 157 of 212 species detected in the macroplots in 2006.

We did not detect a significant difference in the mean proportion of annual forb species between herbaceous- and blue oak-dominated plots ($t_{73} = 1.03$, $p = 0.31$), but we did detect a significant difference in the mean proportion of annual grass species ($t_{73} = 2.28$, $p < 0.05$) (*fig.* 2). Plots under the blue oak canopy had a significantly greater proportion of annual grasses ($P_{AG} = 0.347$) than plots in herbaceous-dominated areas ($P_{AG} = 0.287$). We also detected a significant difference in mean proportions of native species between plots in different vegetation community types ($t_{73} = 8.63$, $p < 0.001$). Plots in herbaceous-dominated areas had a significantly greater proportion of native species ($P_{NATIVE} = 0.492$) than plots under the blue oak canopy ($P_{NATIVE} = 0.214$).

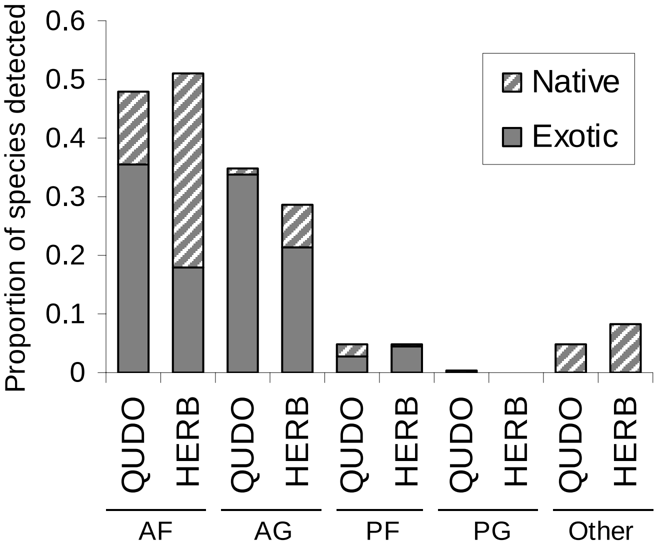

Figure 2—Mean relative cover of different functional guilds for the 14 herbaceous plots (HERB) and 61 blue oak-dominated plots (QUDO) in 2006. (AF = annual forb, AG = annual grass, PF = perennial forb, PG = perennial grass, Other = ferns, non-graminoids and shrubs.)

Overall, we detected medusahead on 64 percent of plots, ranging from 31 percent of plots on Ranch A to 100 percent of plots on Ranch E. We found significant differences in the relative cover of medusahead among properties ($F_{4,72} = 11.61$, $p < 0.001$). Medusahead accounted for a significantly greater proportion of detections on Ranch E ($P_{TCM} = 0.170$) and Ranch C ($P_{TCM} = 0.100$) than on the other three properties (*fig.* 3).

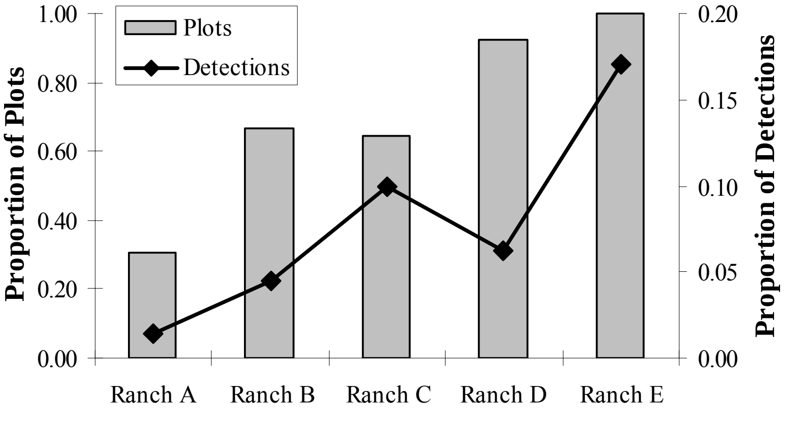

Figure 3—Prevalence of medusahead (*Taeniatherum caput-medusae*) on all properties from pooled data for 2005 and 2006.

We detected yellow star thistle on 9 percent of plots on all properties, ranging from no plots on Ranch E to 25 percent of plots on Ranch B. We did not find a significant difference in the relative cover of yellow star thistle among properties ($F_{4,72} = 0.582$, $p = 0.68$). We did not find the invasive species goat grass (*Aegilops triuncialis*) or false brome (*Brachypodium distachyon*).

Blue oak seedlings were found in 69 percent of all plots. We found significant differences in the presence of blue oak seedlings among properties on blue oak woodland plots ($\chi^2_{4,56} = 10.54$, $p = 0.03$). Of blue oak woodland plots, 100 percent contained a blue oak seedling on Ranch E in either 2005 or 2006, followed by 91 percent on Ranch D, 71 percent on Ranch A, 64 percent on Ranch B, and 60 percent on Ranch C.

Ordination—Community Composition

The NMS ordination plot indicates the structure of species composition by vegetation type (*fig.* 4). The three environmental variables that had the strongest correlation with the ordination axes were slope, percent hardwood canopy cover, and percent cover of bare ground. Elevation, aspect, shrub percent cover, total vegetation cover, and rock cover were not influential factors in the ordination analysis, with r^2 values less than 0.2.

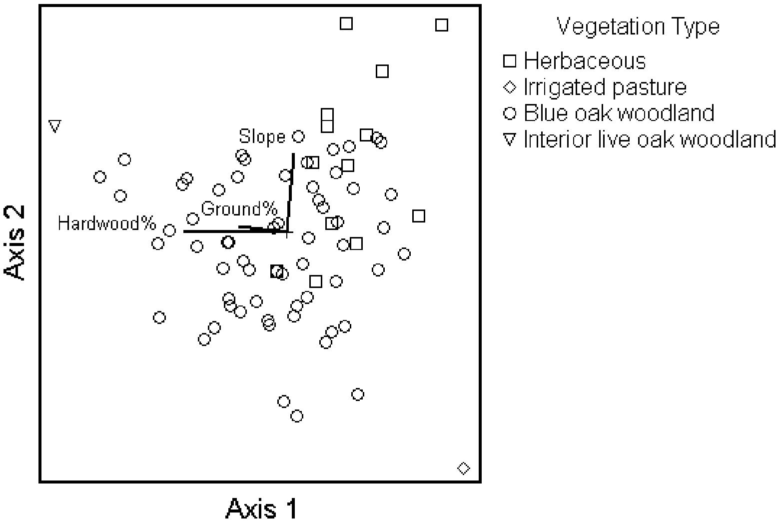

Figure 4—Nonmetric multidimensional scaling graph. Plots farther apart have greater differences in species composition. The three environmental variables depicted in the chart are correlated with species composition.

The NMS model indicated that herbaceous plots share the composition of dominant species. As we expected, cover of hardwood vegetation, mostly blue oaks, was strongly correlated with understory species composition. Our final model had a stress level of 15.95, which is typical for ecological research; values above 20 indicate questionable models (McCune and Grace 2002).

Sampling Effort and Error

The mean sample accumulation curve for all plots in 2006 had a positive slope (*fig. 5*), indicating that point-intercept surveys were not adequate to detect the complete species community present in the plot.

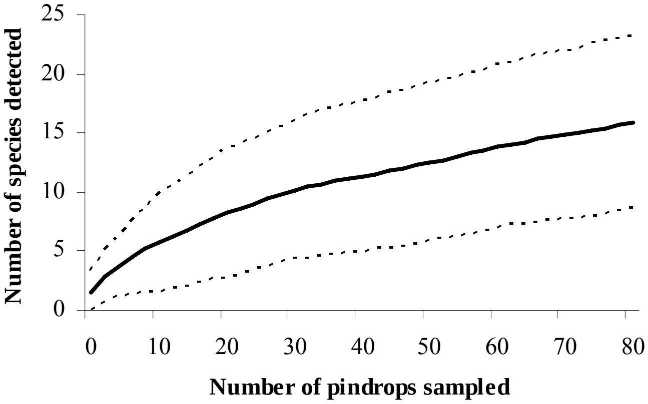

Figure 5—Species accumulation curve for point-intercept surveys, averaged for all plots in 2006. The mean and 95 percent confidence intervals of the cumulative number of species detected are plotted against the number of points sampled in each plot.

Point-intercept surveys identified a mean of 36 percent of species found in the macroplot (*table 1*). In order to detect all species with point-intercepts that we found in the macroplots, we estimated needing to increase our effort from 81 to approximately 80,000 hits per plot.

Table 1—*Mean numbers of species detected in macroplots and with point-intercept surveys in 2006. On average, point-intercept surveys detected 36 percent of species identified in macroplots*.

Property	n (Plots)	Macroplots (Mean/plot)	Point-intercept (Mean/plot)
Ranch A	26	47.1	16.1
Ranch B	12	42.0	15.7
Ranch C	14	45.6	15.9
Ranch D	13	39.1	15.1
Ranch E	12	38.1	14.0
Mean	15.4	42.4	15.3

We found substantial error in the species detected between years; a mean of 55 percent of total species detected at each plot were found in both the 2005 and 2006 macroplot surveys (*table 2*).

Table 2—*Between-year variation in species detected in macroplot surveys. "Total species" is the total number of unique species detected in a plot over two years (2005 and 2006), and "shared species" is the number of those species that were detected in both years. The mean proportion of species shared between 2005 and 2006 is 0.55 for all properties.*

Property	n (Plots)	Total species (Mean/plot)	Shared species (Mean/plot)	P(Shared) (Mean/plot)
Ranch A	24	59.3	34.6	0.58
Ranch B	12	50.8	29.9	0.59
Ranch C	13	56.1	33.0	0.61
Ranch D	12	53.6	27.9	0.52
Ranch E	12	54.3	25.0	0.46
Mean	14.6	54.8	30.1	0.55

Proportion of overlap in species found each year was correlated with difference between the date sampled each year ($r^2_{adj} = 0.14$, $p = 0.001$). This relationship is driven by six plots sampled in early April 2005 and mid May 2006. We expected that a higher level of confidence in returning to the same spatial location as the previous year's plot would be significantly correlated with the proportion of shared species, but this was not the case, even when the effect of difference in date sampled was accounted for in the model ($F_{2,68} = 0.91$, $p = 0.34$).

Discussion

Species Diversity and Functional Guilds

Like most California oak woodlands, the properties we surveyed were dominated by non-native annual grasses and forbs but still contained considerable richness of native species, particularly native annual forbs. The species richness we detected is consistent with an estimate of species richness for grazed California oak savannah (Keeley and Fotheringham 2003). Total plant richness did not differ significantly among properties, although some properties showed differences in functional guilds. Ranch A, located at lower elevation and farther south than Ranches B-E, had a higher proportion of annual forbs and lower proportion of annual grasses than the other ranches, perhaps because of its thinner soils and steeper slopes.

California oak woodlands have experienced dramatic shifts in dominant species over the past century (Heise and Merenlender 2002). While we found considerable variability in species composition between years, the dominant species remained consistent. Our sampling design provides a quantitative estimate for dominant species abundance that can be used as a baseline for future change.

Conservation of blue oaks and native plants are both important goals for easement acquisitions. We found that native plant richness is highest in plots without blue oak canopy. Because these two conservation goals are not compatible at small spatial scales, the properties best able to meet both of these goals will contain a patchwork of blue oak stands and herbaceous areas of high native diversity.

Medusahead and Yellow Star Thistle

Identifying infestations of problematic invasive plants such as medusahead and yellow star thistle can help managers and landowners direct prescribed fire and grazing management programs. Medusahead is widespread on the properties, while yellow star thistle is less common and variable among properties. One study of experimental grazing and fire treatments on Lassen foothills easements indicates that medusahead can be reduced through early summer prescribed burning and winter-spring grazing programs although effects vary by site and native richness may not increase in the short-term (Caroline Christian unpublished data). Communities with lower functional diversity may be more susceptible to invasion from yellow star thistle (Zavaleta and Hulvey 2004) although the relationship between species diversity and invasion appears to be scale dependent (Davies and others 2005).

The absence of goat grass or false brome either on- or off-plot provides important baseline information. Because goat grass can thrive in poor, thin soils it poses a significant threat to the areas of highest plant diversity on the easement properties (DiTomaso and others 2001).

Rare Species and Blue Oak Regeneration

The study was not explicitly designed to sample habitat for rare species, but several rare plants were detected in or between plots, including three California Native Plant Society list 4.3 species, *Polygonum bidwelliae*, *Mimulus glaucesens*, and *Astragalus pauperculus*. Regeneration and recruitment of blue oaks is another significant issue in California oak woodlands, as several studies report a decline in blue oak woodlands due to adult mortality without sufficient recruitment of young oak trees (for example, Bartolome 1987). Blue oak seedlings were common in woodland plots but we found few blue oak, interior live oak, grey pine, or buckeye saplings. Further study of oak woodland population structure could indicate the rates of oak regeneration and oak mortality on the easement properties.

Ordination

Slope, hardwood percent cover, and bare ground cover were significant factors in the ordination analysis of understory community composition. Plots in pasture and interior live oak woodland were clearly separated in composition from the other plots. Some herbaceous plots shared similar species composition as plots under a blue oak canopy, but most had distinctive species composition that separated them from blue oak plots. Other factors we did not measure that could be significant in an analysis of environmental variables include soil moisture, soil depth, soil nutrients, fire history, and current and historic grazing pressure.

Sampling Error and Data Limitations

Improving monitoring protocols requires an understanding of the limitations of collected data. The point-intercept sample-effort curves continued to rise, indicating that the point-intercept method did not capture all understory species within the blue oak woodland and herbaceous communities. We did not anticipate quantifying all species with the point-intercept analysis, and therefore complimented the quantitative point-intercept surveys with the qualitative macroplot, as well as an off-plot species list for understory plants not observed in the plots. One major source of error in comparing data between years is that some landowners did not want permanent markers left on their ranches—52 percent of plots were relocated using only a GPS location, and could have been 10 m from their location the previous year. While this was not a significant variable in the analysis of species difference between 2005 and 2006, it clearly limits the ability to detect change over time using plot data. We were ultimately able to mark plots at the end of the study, using either tree tags or buried metal objects, in addition to site establishment photos, which will allow the plots to be relocated in future years. Differences in phenology between years could also cause errors in detection of species change. Working on private land presents many challenges for site access, including the added logistical difficulty of revisiting sites at the optimal time to match phenology between years. In this case, The Nature Conservancy facilitated ecological research on the easement properties, but not all non-profit or government easement holders have the right to undertake such monitoring on their conservation easements.

Recommendations for Conservation Easement Monitoring in Oak Woodlands

Repeatable ground vegetation measurements are of great value as baselines for conservation areas, and early investment in this type of data is critical. Monitoring should be long term, and permanent plot markers should be considered to allow for greater change detection over time. Allowances for permanent plot markers could become a standard part of conservation easements agreements in which protection of understory diversity is an important concern. Although the availability and quality of satellite imagery and aerial photography will continue to improve over time, understory species diversity must be captured through field surveys in a relatively short time window during the peak blooming season. California oak woodlands have high inter-annual variability and are a non-equilibrium system in which changes in plant cover are expected to follow a state and transition model with steady vegetative states punctuated by rapid changes in plant composition (Jackson and Bartolome 2002, Westoby and others 1989). Design of a monitoring program must therefore anticipate high variability at a small spatial scale as well as the possibility of dramatic shifts in vegetation composition.

One drawback for selecting random sites for avian point counts and then using these points for vegetation sampling was that some plots were heterogeneous from a plant community perspective. When combining bird and plant sampling, it may be important to design the sampling first with plants in mind as they respond to finer changes in geology and overstory composition and then locate the plots far enough apart to allow for independent avian point counts.

Combining the point-intercept method with an inventory of all plants in a plot provides an efficient quantitative estimate of cover and a complete species list that is more likely to capture rare species. In addition, this type of monitoring can provide important information on change in species diversity and abundance over time. Evaluating easement effectiveness in protecting biodiversity may also require research on grazing and fire effects to determine the causes of biodiversity change in combination with long-term monitoring data. It is reasonable to expect that land management practices influencing plant diversity could be controlled by a conservation easement. However, landscape scale changes from climate change, species invasions, and pollution may be beyond the reach of an easement to control. Understory diversity surveys in oak woodlands can provide an important baseline for future change and help quantify the benefits of conservation easements as a conservation strategy.

Acknowledgements

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Continue

Oaks 2040: The Status and Future of Oaks in California[1]

Tom Gaman[2] and Jeffrey Firman[2]

Abstract

California oaks are seriously threatened as a burgeoning state population makes ever more use of the wildland. Most California oaks are not covered by the Forest Practice Act, they are located on private lands, and are potentially at risk. The Oak Woodland Conservation Act of 2004 requires cities and counties to assess their oak resource and to adopt Oak Woodland Management Plans in order to meet their needs for healthy watersheds**.** Therefore, *Oaks 2040* is designed to provide localized information for planners. This paper presents a forest and woodland map of the 10 oak types found in California. The most recent statewide forest survey data from the Forest Inventory and Analysis (FIA) program are compiled into an inventory. The inventory data are then merged to describe the mapped oak types. By merging this inventory with state urban growth projections, we examine which oak woodlands are most likely to face development between now and 2040. Findings are reported for each of six regions: North Coast, North Interior, Central Coast, Sacramento, San Joaquin, and Southern.

Keywords: At-risk, Calveg, FIA, GIS, inventory, oak forest, oak habitat, oak woodland.

Introduction

Developing Planning Tools for Oak Futures in California

Ecological functions, wildlife habitat, recreational opportunities, and scenic values are seriously impaired as population densities and other landscape use pressures increase. Managers of oak woodlands and forests need to balance the biological, sociological, and economic interests of private landowners, public agencies, businesses, universities, environmental groups, and concerned individuals. Planning must address the complexities of local, regional, and statewide oak issues within the context of practical on-the-ground land use decisions.

Oaks 2040 is based on field data and is designed to serve decision makers who may develop local and regional Oak Woodlands Management Plans or advance other conservation strategies. A statewide map of oak distribution and current forest and woodland inventory tree plot data, created by state and federal researchers, were the starting points for *Oaks 2040*. From those, regional analyses of forest structure and oak types as well as region-specific oak inventory summaries have been developed.

Previous work has provided information on the distribution and inventory of California's oak woodlands. Bolsinger (1988) prepared a benchmark publication on the nature, extent, inventory and many uses of California's oak woodlands. Waddell and Barrett (2005) provided a detailed inventory of California oak woodlands, based on data from the early 1990s. This paper is the first to use the new Forest Inventory

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[1] An abbreviated version of this paper was presented at the Sixth California Oak Symposium: Today's Challenges, Tomorrow's Opportunities, October 9-12, 2006, Rohnert Park, California.

[2] Forest Data, P.O. Box 276, Inverness, CA 94937. e-mail: tgaman@forestdata.com, jfirman@forestdata.com.

and Analysis program (FIA 2005) data and recent statewide GIS products, including the Fire and Resource Assessment Program (FRAP 1994-2005). Merenlender and others (2005) developed a complex model to evaluate exurban development threats to wildlands in Sonoma County. Because it relies on general planning information that varies among counties, their model would be difficult to apply statewide. We are not aware of any approach that evaluates urbanization threats to oaks statewide. We used a direct methodology that overlays the combined vegetation map with current state urban growth projections. *Oaks 2040* identifies the location and extent of oaks most at risk of urban development statewide. We do not address other threats to oak woodlands, such as habitat fragmentation, very low residential development, and conversion of woodlands to intensive agriculture.

Methods

Mapping Oak Types

A number of overall vegetation maps, maps of hardwoods in general, and oak-specific maps have been generated over the years. Currently, the most reliable statewide vegetation map available is the LCMMP Vegetation Map (FRAP map), produced by the California Department of Forestry and Fire Protection's Fire and Resource Assessment Program (2003), in conjunction with the U.S. Forest Service Region 5 Remote Sensing Lab in Sacramento. While these maps do not focus specifically on oaks, oak habitat types can be extracted from mapped vegetation types. Using the FRAP map as a foundation (supplemented by other earlier mapping efforts), we have generated species-specific range maps of oak types throughout the state.

The FRAP map uses the Calveg classification system which first divides all vegetation into "covertype." For finding wildland oak habitat, only two covertypes are relevant. All woodland classified as hardwood (HDW) or forest classified as conifer/hardwood mix (MIX) can potentially be oak habitat, provided it contains the relevant hardwood species. All other covertypes were eliminated from the analysis.

After covertype, the Calveg system also specifies "vegtype," which identifies the dominant species association. For both HDW and MIX covertypes, the data were screened to ensure that the hardwood associations being mapped in a particular location are oaks. Nine such associations are dominated by a single species, each forming its own oak habitat type, or "oak type." Three heterogeneous hardwood types were combined to generate a "mixed" oak type. The 10 resulting oak types, each potentially occurring in both "woodlands" and "forests,"[3] are listed in *table 1*.

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[3] "Oak woodlands" are considered to be those mapped vegetation types where oaks dominate the landscape. "Oak forests" include oaks, but oaks may not necessarily be among the dominant species. By definition, forests and woodlands must have at least 10 percent canopy cover and be at least 1 hectare in extent.

Table 1—*Oak types.*

Oak Type	Scientific Name	Calveg Type(s)
Black Oak	*Quercus kelloggii*	QK
Blue Oak	*Quercus douglasii*	QD
Canyon Live Oak	*Quercus chrysolepis*	QC
Coast Live Oak	*Quercus agrifolia*	QA
Engelmann Oak	*Quercus engelmannii*	QN
Interior Live Oak	*Quercus wislizeni*	QW
Oregon White Oak	*Quercus garryana*	QG
Tanbark Oak	*Lithocarpus densiflorus*	QT
Valley Oak	*Quercus lobata*	QL
Mixed Oaks	not applicable	EX/NX/TX

This selection and reclassification process was applied to the FRAP maps. The results are GIS layers and maps depicting the distribution of woodland and forest oak habitat types throughout the state of California. See the tables in Appendix A for acres of cover in which oaks dominate the woodland by county and oak type and acres of cover in which oaks are present in the forest by county and oak type.

Ownership and Risk Analysis

The land ownership data are courtesy of the California Department of Forestry's Forest and Rangeland Resources Assessment Program. Using their layer, the state is divided into a variety of public and private ownership categories. The statewide ownership layer overlaid on top of the oak type map reveals ownership patterns among California's oaks.

The development risk data have been derived from Fire and Resource Assessment Program (FRAP) development projections (1994-2005). This dataset is based on California Department of Finance and U.S. Census data. This layer tracks past development by decade and predicts future development through 2040. Using this information, three categories were defined. "Developed" is defined as anything that was developed (greater than 32 housing units per square mile) by 2000. "At risk" refers to anything that was not developed by 2000 but is expected to develop by 2040. And "stable" refers to anything that was not developed by 2000 and is unlikely to develop before 2040. Once the layer was divided into these three categories, it was overlaid on top of the oak type map. The oak woodlands of the state were thereby divided into groups by oak type, ownership, and development risk.

Inventory and Analysis

The other critical element for assessment of mapped oak types is the inventory summary, which is based upon data obtained from the U.S. Forest Service's Forest Inventory & Analysis Program (2005; see also http://fia.fs.fed.us/tools-data/). This statewide grid of permanent forest survey sample "plots" yields information about what the mapped oak forests and woodlands look like on the ground. The plots provide information not obtainable via remote sensing techniques—an inventory of forest fuels, species distribution, specific size, growth, regeneration, habitat features, pests, and disease. With point-specific data ranging from species composition to seedling regeneration to tree size and density, these plots help one understand the makeup of each of the 10 oak types.

The 2001-2004 FIA field data were obtained to provide an inventory of each of the oak types discussed above. Combining the ground-based survey data and the GIS mapping data enabled us to provide a new comprehensive oak inventory as shown in Appendix B.

California Oaks: The Statewide Analysis

California has approximately 8.5 million acres of oak woodland and 4.5 million acres of oak forest. These 13 million acres comprise more than one-eighth of the state's area (*fig*. 1). To facilitate statewide analysis, California counties have been grouped into six distinct regions (*fig*. 2), each of which is discussed later in this report. The Sacramento and San Joaquin regions are home to more than half of California's oak woodland. Oak forests are concentrated in the North Coast and North Interior regions. California currently has approximately two billion oaks greater than 1 inch DBH. More than 800 million of these oaks are larger than 5 inches DBH.

Figure 1—California oak forests and woodlands.

Figure 2—California counties are grouped into six regions.

California oaks are diverse. Blue oak (see *table 1* for scientific names of species) is California's dominant oak species, representing more than one-third of the state's oak woodlands. Canyon, coast and interior live oak woodlands comprise approximately one-third of California's oak woodlands. Tanbark, black and canyon live oak forests account for more than 80 percent of California oak forests.

In oak woodland, oaks comprise 60 percent of the total tree basal area, 67 percent of trees greater than 5 inches DBH and 37 percent of trees greater than 24 inches DBH. In oak forest, oaks comprise 18 percent of the total tree basal area, less than 24 percent of trees greater than 5 inches DBH and 8 percent of trees greater than 24 inches DBH. Blue oak, Oregon white oak and, to a lesser extent, interior live oak, are regenerating poorly. Blue oak averages about one seedling per thousand square feet in woodlands, and less than one seedling (1 foot or more in height) per two established oak trees. Not a single Engelmann oak or valley oak seedling was tallied on any of the 932 FIA plots.

Oaks 2040: Future Prospects for California's Oaks

The FRAP development models forecast that more than one million acres of California's oak woodlands are developed, and approximately 750,000 are at risk of urban development before 2040. Twenty percent of California's oak woodlands are facing rapid and increasing urbanization by 2040. The oak woodlands of the Central Valley and Sierra Foothills face the most immediate threats. Eighty percent of California's oak woodlands that are at risk of development are located in the Sacramento and San Joaquin regions. *See figure 3*.

Figure 3—California oak woodlands at risk of development.

California Oaks: The Regional Analyses

This section provides regional summaries. Each describes oak distribution, oak woodland and oak forest diversity, and oaks at risk.[4]

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[4] Appendix B summaries are further detailed by region in the full report online at http://www.californiaoaks.org/Oaks2040.

North Coast Region

Counties included in this region are Del Norte, Humboldt, Mendocino, and Sonoma.

Oak Distribution and Diversity

The North Coast Region has 1.3 million acres of oak woodland and 1.5 million acres of oak forest. In fact 35 percent of California's oak forest is found in the North Coast region, and oaks are present on 45 percent of the region's land (more coverage than any other region). In the North Coast region, there are 245 million oaks greater than 5- inches DBH. Only the Central Coast tops the North Coast's two million oaks with DBH greater than 24 inches.

The North Coast oak woodlands feature Oregon white oak, tanbark oak and mixed oak. Canyon live oaks and California black oaks are also present, mixing in with Douglas-fir (*Pseudotsuga menziesii*), Pacific madrone (*Arbutus menziesii*), and California bay (*Umbellularia californica*). Oaks comprise approximately one-half of the basal area, trees/acre, and trees greater than 5 inches DBH/acre in white oak woodlands. In tanbark oak woodlands, oaks comprise less than 20 percent of the basal area, trees/acre, and trees greater than 5 inches DBH/acre.

In the North Coast's oak forests, tanbark oak is predominant. Associated species include Douglas-fir, redwood (*Sequoia sempervirens*), madrone, bay, canyon live oak and California black oak.

Oaks at Risk in the North Coast Region

In terms of ownership, 84 percent of the North Coast's oak woodlands are located on private property. Most of the remainder is owned by the U.S. Forest Service and various other federal government agencies. Private ownership of oak woodland increases moving southward, ranging from 40 percent in Del Norte County to 95 percent in Sonoma County.

A total of 8 percent of North Coast oak woodlands have already been developed and 4 percent are at risk of near-time urban development, according to the FRAP forecasting model.

North Interior Region

Counties in this region are Lassen, Modoc, Shasta, Siskiyou, and Trinity.

Oak Distribution and Diversity

Nearly 1 million acres of oak woodland and 1.1 million acres of oak forest reside within the North Interior. The North Interior and the North Coast are the only two regions with more oak forest than oak woodland. The North Interior has nearly 400 million oak trees, and 150 million of these oaks are greater than 5 inches DBH.

In this region, a balanced mixture of blue oak, California black oak, canyon live oak and Oregon white oak woodlands is found. Blue oak woodlands typically include gray pine (*Pinus sabiniana*) and either interior or coast live oak, and oaks comprise more than 80 percent of the basal area and more than 90 percent of the trees. Oregon white oak woodlands include black oak, Douglas-fir, and ponderosa pine (*Pinus ponderosa*), and oaks make up 40 percent of the basal area and more than half of the trees greater than 5 inches DBH. In black oak and canyon live oak woodlands, oaks comprise 50 percent of the basal area and 70 percent of the trees greater than 5 inches DBH.

In the North Interior oak forests, canyon live oak and black oak are prominent. These two oak species mix in with the local conifer species, including Douglas-fir, ponderosa pine, sugar pine (*Pinus labertiana*) and madrone. In black oak forests, oaks comprise one-fifth of the basal area. One-third of the trees greater than 5 inches DBH are oaks.

Oaks at Risk in the North Interior Region

In terms of ownership, 60 percent of North Interior oak woodlands are privately owned,and 10 percent of the region's oak woodland has already been developed. A total of 3 percent is at risk for urban development by 2040. We project that 87 percent is unlikely to develop into urban and suburban uses before 2040. Shasta County oak woodland is most at risk, as 15 percent has been developed and 5 percent more may develop by 2040.

Central Coast Region

Counties included in this region are Alameda, Contra Costa, Marin, Monterey, San Benito, San Francisco, San Luis Obispo, San Mateo, Santa Barbara, Santa Clara, Santa Cruz, Solano, and Ventura.

Oak Distribution and Diversity

The Central Coast is home to 1.6 million acres of oak woodlands and 300,000 acres of oak forests. Oaks are present on 17.5 percent of the region's area. There are 87 million oaks 5 inches DBH and larger within the region.

One-half of the Central Coast's oak woodland is coast live oak, and one-third is blue oak. A total of 80 percent of California's coast live oak woodland is in the Central Coast, and 30 percent of the state's valley oak woodland is in the Central Coast. However, there is not adequate inventory data to confidently describe this critical oak type.

Tanbark oak and coast live oak account for three-quarters of the region's oak forests. Redwood and Douglas-fir dominate in these forests, but 40 percent of the trees are oaks.

Oaks at Risk in the Central Coast Region

A complex land ownership matrix covers the oak woodlands of the Central Coast. Private ownership of oak woodlands predominates, averaging 75 percent throughout the region and ranging from 65 percent in Santa Barbara County to 95 percent in Alameda County. The Los Padres National Forest includes much of the oak woodlands in Ventura, Santa Barbara, San Luis Obispo, and Monterey counties. Additionally, the Bureau of Land Management manages 20 percent of San Benito's oak woodlands, and Fort Hunter-Liggett holds 12 percent of Monterey's oak woodlands. The state owns approximately 10 percent of oak woodland in Santa Clara, Contra Costa, and Santa Cruz counties.

Almost 85 percent of the Central Coast oak woodlands are unlikely to be developed before 2040. Most of the remaining areas have already been developed. Less than 3 percent is at current risk for urban development.

Sacramento Region

Counties in this region include Butte, Colusa, El Dorado, Glenn, Lake, Napa, Nevada, Placer, Plumas, Sacramento, Sierra, Solano, Sutter, Tehama, Yolo, and Yuba.

Oak Distribution and Diversity

The Sacramento region's 2.1 million acres of oak woodlands provide nearly one-quarter of the state's total. Oaks are present on 20 percent of the region's land. There are more than 165 million oak trees >5 inches in diameter in this region.

More than half of the Sacramento region's oak woodlands are blue oak. Gray pines mix in, but oaks comprise 70 percent of the basal area and 80 percent of the trees greater than 5 inches DBH. The region contains more than one-third of the state's blue oak woodland.

Interior live oak woodland contains blue oak, valley oak, California black oak, gray pine, and ponderosa pine. Canyon live oak and black oak woodlands include Douglas-fir, ponderosa pine, and incense cedar (*Calocedrus decurrens*). In canyon and interior live oak woodland, oaks make up 80 percent of the basal area and 90 percent of the trees. The Sacramento region has more than one-third of California's valley oak woodland.

Black oak and canyon live oak dominate the region's oak forests. Canyon live oak forests are 60 percent oaks, mixing with ponderosa pines and Douglas-firs. Black oak forests are 25 percent oaks, along with Douglas-fir, ponderosa pine, white fir (*Abies concolor*), and incense cedar.

Oaks at Risk in the Sacramento Region

More than 80 percent of the Sacramento region's oak woodland is privately owned. The U.S. Forest Service owns about 60 percent of the remaining public lands.

The Sacramento region is more at risk for development than any other. Only two-thirds of the oak woodlands are considered "stable." One-sixth is developed and one-sixth is at risk. More than 300,000 acres of oak woodland could be developed in the Sacramento region by 2040.

El Dorado County has more oak woodlands at risk than any other county in the state, but Tehama, Butte, and Yuba counties are not far behind. By 2040, 80 percent of El Dorado's oak woodlands and more than half of the oak woodlands in Nevada, Yuba, and Placer counties may be developed.

San Joaquin Region

Counties in this region are Alpine, Amador, Calaveras, Fresno, Inyo, Kern, Kings, Madera, Mariposa, Merced, Mono, San Joaquin, Stanislaus, Tulare, and Tuolumne.

Oak Distribution and Diversity

The San Joaquin region has more than 2.3 million acres of oak woodlands and 500,000 acres of oak forests. Oaks are present on only 10 percent of the region's land; however, certain portions of the region have far greater oak woodland density than others. Twenty-seven percent of the state's oak woodland fall within these 15 counties. The San Joaquin region currently has 113 million oaks larger than 5 inches DBH.

More than half of the region’s oak woodlands are blue oak and another 25 percent are interior live oak. Associated species include gray pine and California buckeye (*Aesculus californica*), as well as valley oak, blue oak and canyon and interior live oaks. The San Joaquin region has more blue oak woodlands and interior live oak woodlands than any other region. In blue oak woodlands, oaks account for 70 percent of the trees, 80 percent of the basal area, and trees greater than 5 inches DBH. In interior live oak woodlands, oaks provide 70 percent of the tree basal area and more than 80 percent of the trees. In canyon live oak woodlands, oaks comprise 55 percent of the basal area, 62 percent of all trees, and 67 percent of trees greater than 5 inches DBH.

Canyon live oak and California black oak comprise almost 90 percent of the oak forests. Associated species in San Joaquin oak forests include incense cedar, ponderosa pine, sugar pine and white fir. In canyon live oak forests, oaks provide one-third of the basal area and nearly one-half of the trees. In black oak forest, oaks comprise more than half of the trees, but only one-third of the trees greater than 5 inches DBH and only one-quarter of the tree basal area.

Oaks at Risk in the San Joaquin Region

Seventy-three percent of the San Joaquin region’s oak woodlands are privately owned. The U.S. Forest Service owns 18 percent and the Bureau of Land Management owns 5 percent. A total of 10 percent of the oak woodlands in the region have already been developed, and 10 percent are at high risk of development by 2040. Eighty percent are currently stable; however, targeted planning could ensure that a greater number of acres are conserved for the long-term. Nearly 250,000 acres of oak woodlands in the San Joaquin region are at risk of development by 2040. Only the Sacramento region contains more oak woodlands at risk. In Madera, Amador, and Calaveras counties combined, more than one-third of all oak woodland may be developed before 2040.

Southern Region

Counties in this region are Imperial, Los Angeles, Orange, Riverside, San Bernardino, and San Diego.

Oak Distribution and Diversity

The Southern region is home to more than 300,000 acres of oak woodlands and more than 200,000 acres of oak forests. Combined, these 500,000 acres comprise only 2 percent of the region. However, discounting urban areas and the desert, the oak woodland concentration is much higher.

Coast live oak and canyon live oak are most prevalent, but California black oak and Engelmann oak populations are also significant. Eighty-five percent of the basal area is comprised of oaks. The region has 23 million oak trees > 5 inches DBH. The rare Engelmann oak is found only within this region, mostly in San Diego County.

Canyon live oak and black oak dominate in the Southern region’s oak forests.

Oaks at Risk in the Southern Region

The oak woodlands of the Southern region have the highest levels of public ownership found in the state. The U.S. Forest Service owns 44 percent of the region’s oak woodlands, 11 percent are owned by other government agencies, and 45 percent are privately owned.

A total of 20 percent of the Southern region's oak woodlands have already been developed, and 10 percent are at risk of development by 2040. Development of the remaining 70 percent is not anticipated in the near future. Oak woodland development percentages are higher than in any other region in the state.

Summary

The project presents an updated map and inventories of oak forests and woodlands. These data should be useful for conservation planning at the regional, county, and local levels. The FIA plots are also valuable for ongoing monitoring of thousands of individual trees and populations on a landscape scale over a long period of time.

We found that large oak trees are deceptively rare in California. Valley oak and Engelmann oak types need more intensive inventories. Blue oak woodland species have unsustainable rates of regeneration.

Oak woodlands in the Sacramento and San Joaquin regions are most at risk of development. California should plan for protection of its "stable" oak ecosystems now before these ecosystems are fragmented beyond repair.

A more-detailed version of this report, including regional inventories, is presented online at the Web site of the California Oak Foundation http://www.californiaoaks.org/Oaks2040.

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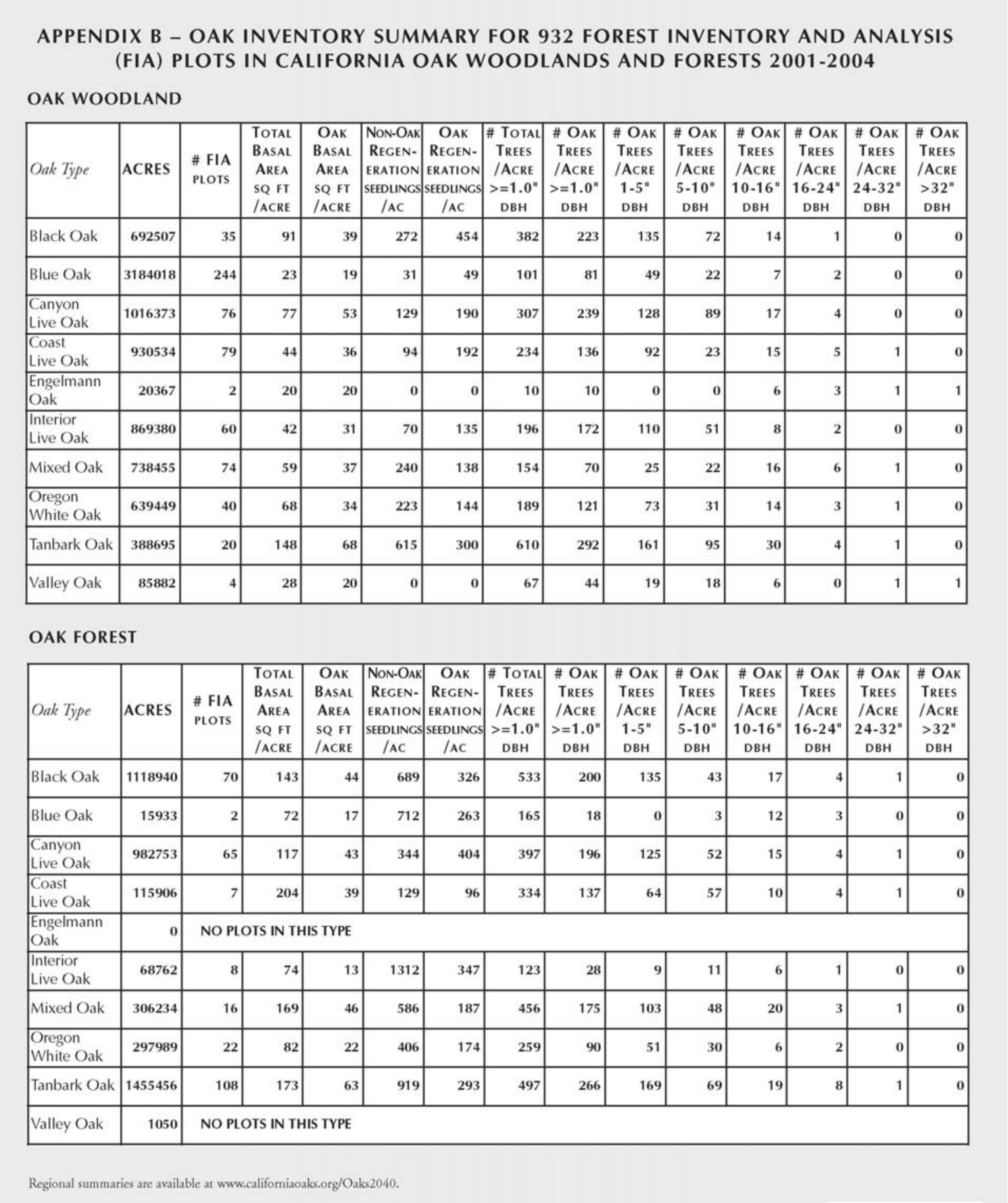
APPENDIX A – ACRES OF COVER WHERE OAKS DOMINATE THE WOODLAND BY COUNTY AND OAK TYPE

REGION	COUNTY	OAK TYPE										
		Black Oak	*Blue Oak*	*Canyon Live Oak*	*Coast Live Oak*	*Engelmann Oak*	*Interior Live Oak*	*Mixed Oak*	*Oregon White Oak*	*Tan Oak*	*Valley Oak*	*Total Acres*
North Coast	Del Norte	84	0	1,011	0	0	0	2,939	355	42,778	0	47,168
	Humboldt	16,671	0	20,831	10	0	0	13,572	100,484	153,873	0	305,442
	Mendocino	49,553	12,040	60,603	863	0	16,715	119,231	283,036	104,631	4,206	650,879
	Sonoma	3,212	524	7,354	21,601	0	1,484	176,852	41,124	30,402	524	283,077
North Interior	Lassen	7,965	0	0	0	0	0	0	438	0	0	8,403
	Modoc	737	0	0	0	0	0	0	369	0	0	1,106
	Shasta	170,028	268,857	83,918	0	0	4,643	46	21,116	336	6,055	554,998
	Siskiyou	13,053	0	57,570	0	0	0	10,141	97,529	5,646	0	183,938
	Trinity	51,154	275	84,077	0	0	0	0	80,692	15,747	11	231,956
Central Coast	Alameda	0	29,273	12	40,340	0	0	28,255	0	0	1,396	99,275
	Contra Costa	30	29,758	50	32,564	0	2,462	5,051	0	0	691	70,605
	Marin	0	310	0	10,383	0	0	36,792	875	0	108	48,468
	Monterey	679	252,092	0	266,145	0	0	12	0	26,776	6,641	552,345
	San Benito	0	61,729	0	44	0	0	753	0	0	8	62,534
	San Luis Obispo	1,773	68,413	92	83,636	0	0	25,419	0	31	8,672	188,035
	San Mateo	0	515	0	15,021	0	0	3,089	0	65	1,403	20,093
	Santa Barbara	0	22,548	26,794	170,970	0	0	0	0	197	2,925	223,435
	Santa Clara	52	58,083	110	74,259	0	0	58,888	0	10	3,543	194,946
	Santa Cruz	0	0	0	22,474	0	0	6,362	0	48	0	28,884
	Ventura	61	151	14,427	49,929	0	0	0	0	0	1,179	65,747
Sacramento	Butte	20,042	100,835	31,037	0	0	46,668	4,045	0	5,031	429	208,084
	Colusa	353	112,868	3,342	0	0	167	0	450	0	1,563	118,741
	El Dorado	35,900	46,247	24,591	0	0	90,549	15,893	0	0	3,708	216,888
	Glenn	5,842	83,184	23,385	0	0	23	0	2,755	0	2,626	117,816
	Lake	23,948	90,203	34,348	42	0	3,508	15,013	7,777	1,091	2,126	178,056
	Napa	1,236	62,243	941	5,719	0	6,682	88,715	1,380	12	1,474	168,400
	Nevada	27,129	34,650	12,328	0	0	49,647	2,686	0	84	2,172	128,697
	Placer	35,541	49,754	41,854	0	0	24,333	12,212	0	0	2,709	166,403
	Plumas	18,543	0	11,730	0	0	0	38	0	102	0	30,413
	Sacramento	0	7,254	0	0	0	789	26	0	0	49	8,119
	Sierra	9,200	8	8,512	0	0	8	3	0	79	0	17,809
	Solano	44	17,365	0	2,010	0	848	6,228	0	0	1,074	27,568
	Tehama	24,505	443,003	46,383	0	0	1,973	0	1,069	71	12,238	529,242
	Yolo	0	78,912	61	9	0	1,313	0	0	0	1,155	81,450
	Yuba	10,459	47,733	4,150	0	0	26,186	527	0	1,685	1,384	92,122
San Joaquin	Alpine	612	0	130	0	0	0	0	0	0	0	742
	Amador	9,360	49,802	12,071	0	0	44,813	5,912	0	0	1,631	123,588
	Calaveras	11,729	112,449	26,552	0	0	42,538	860	0	0	235	194,362
	Fresno	15,929	228,915	41,437	0	0	81,779	22,354	0	0	424	390,838
	Inyo	590	0	3,546	0	0	0	25	0	0	0	4,161
	Kern	16,732	153,891	49,437	10	0	73,062	22,822	0	0	7,059	323,013
	Kings	0	9,576	0	0	0	343	111	0	0	0	10,029
	Madera	9,407	124,132	29,844	0	0	98,561	1,896	0	0	2,320	266,160
	Mariposa	12,317	120,825	42,628	0	0	106,607	684	0	0	798	283,858
	Merced	0	50,868	0	2,411	0	5	3,973	0	0	532	57,790
	San Joaquin	0	17,484	0	424	0	437	1,686	0	0	18	20,049
	Stanislaus	0	104,218	0	1,288	0	1,279	1,074	0	0	181	108,038
	Tulare	43,406	157,740	43,210	0	0	67,799	33,504	0	0	256	345,915
	Tuolumne	18,082	72,807	48,071	0	0	72,308	349	0	0	186	211,803
Southern	Los Angeles	1,596	2,487	60,102	30,790	32	351	970	0	0	2,177	98,503
	Orange	0	0	2,419	10,440	0	0	0	0	0	0	12,859
	Riverside	3,248	0	14,207	12,128	2,371	910	172	0	0	0	33,036
	San Bernardino	11,083	0	33,953	2,534	0	538	761	0	0	0	48,869
	San Diego	10,623	0	9,255	74,491	17,964	54	8,515	0	0	0	120,903
	ALL COUNTIES	692,507	3,184,018	1,016,373	930,534	20,367	869,380	738,455	639,449	388,695	85,882	8,565,659

APPENDIX A – ACRES OF COVER WHERE OAKS ARE PRESENT IN THE FOREST BY COUNTY AND OAK TYPE

REGION	COUNTY	OAK TYPE										
		Black Oak	*Blue Oak*	*Canyon Live Oak*	*Coast Live Oak*	*Engelmann Oak*	*Interior Live Oak*	*Mixed Oak*	*Oregon White Oak*	*Tan Oak*	*Valley Oak*	*Total Acres*
North Coast	Del Norte	1,344	0	1,611	0	0	0	8,762	948	130,743	0	143,408
	Humboldt	18,556	0	32,777	0	0	0	42,345	43,757	519,090	0	656,524
	Mendocino	39,223	544	33,603	484	0	2,100	39,060	69,662	395,741	0	580,416
	Sonoma	675	0	2,618	3,849	0	29	47,157	7,767	68,488	0	130,583
North Interior	Lassen	2,446	0	0	0	0	0	0	0	0	0	2,446
	Shasta	231,378	5,066	48,675	0	0	93	24	13,894	468	0	299,597
	Siskiyou	32,313	0	180,891	0	0	0	73,999	99,747	85,800	0	472,749
	Trinity	76,489	0	130,061	0	0	0	0	49,701	61,739	0	317,989
Central Coast	Alameda	0	0	0	432	0	0	413	0	0	0	844
	Contra Costa	4	286	98	1,042	0	294	236	0	0	0	1,959
	Marin	0	0	0	118	0	0	15,125	0	2,429	0	17,672
	Monterey	0	229	0	24,421	0	0	6	0	26,414	0	51,069
	San Benito	0	50	0	0	0	0	0	0	0	0	50
	San Luis Obispo	1,542	44	0	1,162	0	0	1,775	0	0	0	4,522
	San Mateo	0	0	0	8,113	0	0	2,347	0	46,577	121	57,158
	Santa Barbara	0	0	13,708	4,813	0	0	0	0	0	0	18,521
	Santa Clara	193	36	0	5,080	0	0	4,271	0	5,911	0	15,491
	Santa Cruz	0	0	0	58,378	0	0	7,473	0	50,895	0	116,746
	Ventura	0	0	27,705	801	0	0	0	0	0	0	28,505
Sacramento	Butte	50,365	3,010	28,510	0	0	4,718	9,460	0	41,470	0	137,533
	Colusa	2,088	193	6,071	0	0	0	0	2,551	0	0	10,904
	El Dorado	59,220	157	16,225	0	0	4,155	7,829	0	100	64	87,750
	Glenn	5,522	75	3,954	0	0	0	0	2,483	0	0	12,033
	Lake	17,725	503	18,082	0	0	214	5,601	5,169	284	33	47,612
	Napa	410	68	512	31	0	0	17,396	159	10	0	18,587
	Nevada	75,680	724	18,602	0	0	4,133	407	0	1,328	67	100,941
	Placer	69,336	146	22,150	0	0	752	8,569	0	0	72	101,025
	Plumas	43,057	0	10,980	0	0	0	146	0	237	0	54,420
	Sierra	29,495	0	12,706	0	0	0	84	0	427	0	42,713
	Solano	0	0	0	0	0	6	0	0	0	0	6
	Tehama	32,200	1,004	16,577	0	0	172	0	2,152	61	0	52,166
	Yuba	24,450	86	5,272	0	0	1,725	648	0	17,245	156	49,582
San Joaquin	Alpine	250	0	90	0	0	0	0	0	0	0	340
	Amador	15,502	0	7,446	0	0	3,115	1,644	0	0	47	27,754
	Calaveras	22,842	0	35,566	0	0	13,537	850	0	0	0	72,795
	Fresno	38,798	2,212	37,285	0	0	1,166	65	0	0	0	79,526
	Inyo	173	0	8,147	0	0	0	0	0	0	0	8,320
	Kern	23,428	818	37,609	0	0	572	947	0	0	53	63,427
	Kings	0	213	0	0	0	0	0	0	0	0	213
	Madera	24,728	37	23,870	0	0	5,249	23	0	0	320	54,227
	Mariposa	35,742	34	26,151	0	0	11,900	44	0	0	92	73,964
	Tulare	37,483	9	14,208	0	0	326	631	0	0	0	52,656
	Tuolumne	37,778	83	41,705	0	0	14,112	31	0	0	25	93,736
Southern	Los Angeles	2,863	306	42,577	464	0	14	60	0	0	0	46,283
	Orange	0	0	919	14	0	0	0	0	0	0	933
	Riverside	2,948	0	32,346	183	0	252	0	0	0	0	35,728
	San Bernardino	46,395	0	35,057	32	0	130	151	0	0	0	81,764
	San Diego	16,302	0	8,390	6,490	0	0	8,654	0	0	0	39,836
	ALL COUNTIES	1,118,940	15,933	982,753	115,906	0	68,762	306,234	297,989	1,455,456	1,050	4,363,023



APPENDIX B – OAK INVENTORY SUMMARY FOR 932 FOREST INVENTORY AND ANALYSIS (FIA) PLOTS IN CALIFORNIA OAK WOODLANDS AND FORESTS 2001-2004

OAK WOODLAND

Oak Type	ACRES	# FIA PLOTS	Total Basal Area sq ft /acre	Oak Basal Area sq ft /acre	Non-Oak Regeneration seedlings /ac	Oak Regeneration seedlings /ac	# Total Trees /Acre >=1.0" DBH	# Oak Trees /Acre >=1.0" DBH	# Oak Trees /Acre 1-5" DBH	# Oak Trees /Acre 5-10" DBH	# Oak Trees /Acre 10-16" DBH	# Oak Trees /Acre 16-24" DBH	# Oak Trees /Acre 24-32" DBH	# Oak Trees /Acre >32" DBH
Black Oak	692507	35	91	39	272	454	382	223	135	72	14	1	0	0
Blue Oak	3184018	244	23	19	31	49	101	81	49	22	7	2	0	0
Canyon Live Oak	1016373	76	77	53	129	190	307	239	128	89	17	4	0	0
Coast Live Oak	930534	79	44	36	94	192	234	136	92	23	15	5	1	0
Engelmann Oak	20367	2	20	20	0	0	10	10	0	0	6	3	1	1
Interior Live Oak	869380	60	42	31	70	135	196	172	110	51	8	2	0	0
Mixed Oak	738455	74	59	37	240	138	154	70	25	22	16	6	1	0
Oregon White Oak	639449	40	68	34	223	144	189	121	73	31	14	3	1	0
Tanbark Oak	388695	20	148	68	615	300	610	292	161	95	30	4	1	0
Valley Oak	85882	4	28	20	0	0	67	44	19	18	6	0	1	1

OAK FOREST

Oak Type	ACRES	# FIA PLOTS	Total Basal Area sq ft /acre	Oak Basal Area sq ft /acre	Non-Oak Regeneration seedlings /ac	Oak Regeneration seedlings /ac	# Total Trees /Acre >=1.0" DBH	# Oak Trees /Acre >=1.0" DBH	# Oak Trees /Acre 1-5" DBH	# Oak Trees /Acre 5-10" DBH	# Oak Trees /Acre 10-16" DBH	# Oak Trees /Acre 16-24" DBH	# Oak Trees /Acre 24-32" DBH	# Oak Trees /Acre >32" DBH
Black Oak	1118940	70	143	44	689	326	533	200	135	43	17	4	1	0
Blue Oak	15933	2	72	17	712	263	165	18	0	3	12	3	0	0
Canyon Live Oak	982753	65	117	43	344	404	397	196	125	52	15	4	1	0
Coast Live Oak	115906	7	204	39	129	96	334	137	64	57	10	4	1	0
Engelmann Oak	0	NO PLOTS IN THIS TYPE												
Interior Live Oak	68762	8	74	13	1312	347	123	28	9	11	6	1	0	0
Mixed Oak	306234	16	169	46	586	187	456	175	103	48	20	3	1	0
Oregon White Oak	297989	22	82	22	406	174	259	90	51	30	6	2	0	0
Tanbark Oak	1455456	108	173	63	919	293	497	266	169	69	19	8	1	0
Valley Oak	1050	NO PLOTS IN THIS TYPE												

Regional summaries are available at www.californiaoaks.org/Oaks2040.

Continue

Using Vegetation Type Map Data to Increase Our Understanding of Long-Term Ecological Change in the Woodlands Surrounding San Francisco Bay[1]

Tim Doherty,[2] Barbara Allen-Diaz,[3] and Maggi Kelly[4]

Abstract

In the 1920s and 1930s A.E. Wieslander, a silviculturist with the U.S. Forest Service California (now Pacific Southwest) Forest and Range Experiment Station, and his crew surveyed much of the California landscape. The data they collected, known as the Wieslander Vegetation Type Mapping collection (VTM), contains vegetation data, detailed vegetation type maps, and an extensive photograph collection. We examined VTM plots in the *Quercus agrifolia-Umbellularia californica* woodlands surrounding San Francisco Bay in order to examine the relationships between current and historical stand conditions. We selected 12 VTM plots to resample across a gradient of Sudden Oak Death (SOD) infection. Our initial findings from re-located plots show no significant increase in basal area between sampling dates for any tree species. We identified two distinct plant communities that were independent of sampling date; two of the 12 plots had been converted through management actions. This research required significant coordination and access to private and public lands for re-sampling purposes.

Keywords: Quercus agrifolia, Umbellularia californica, *Wieslander VTM plots.*

Introduction

In the first half of the 20th century, A.E. Wieslander and his crew surveyed much of the California landscape. The data they collected, known as the Wieslander Vegetation Type Mapping collection (VTM), contains vegetation data collected from more than 18,000 plots, roughly 330 colored type maps and more than 3,000 black and white photos. The collection is now available online at http://vtm.berkeley.edu. The digitization and georeferencing process was funded by the USDA Forest Service (Pacific Northwest and Pacific Southwest Research Stations), the USDA Cooperative State Research, Education and Extension Service, University of California Digital Library Project, and the College of Natural Resources at UC Berkeley. The georeferencing process entails assigning map coordinate data to historical VTM plots and topo maps so that they can be used in a geographic information system—GIS (Kelly and others 2005). The VTM collection serves as a valuable public resource to increase our understanding of long-term ecological change within California's

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[1] An abbreviated version of this paper was presented at the Sixth California Oak Symposium: Today's Challenges, Tomorrow's Opportunities, October 9-12, 2006, Rohnert Park, California.

[2] Graduate Student, Department of Environmental Science, Policy and Management, UC Berkeley, Berkeley, CA, 94720. e-mail: tdoherty@nature.berkeley.edu.

[3] Professor, Department of Environmental Science, Policy and Management, UC Berkeley, Berkeley, CA, 94720. e-mail: ballen@nature.berkeley.edu.

[4] Associate Professor and UCCE Specialist, Department of Environmental Science, Policy and Management, UC Berkeley, Berkeley, CA, 94720.

dynamic vegetation communities. We are particularly interested in understanding decades-long change in the woodlands surrounding San Francisco Bay, which is dominated by coast live oak (*Quercus agrifolia*) and California bay (*Umbellularia californica*) (*fig.* 1). Using the VTM data provided a unique opportunity to examine change in species composition, stand structure, and community stability over a period of 70 years.

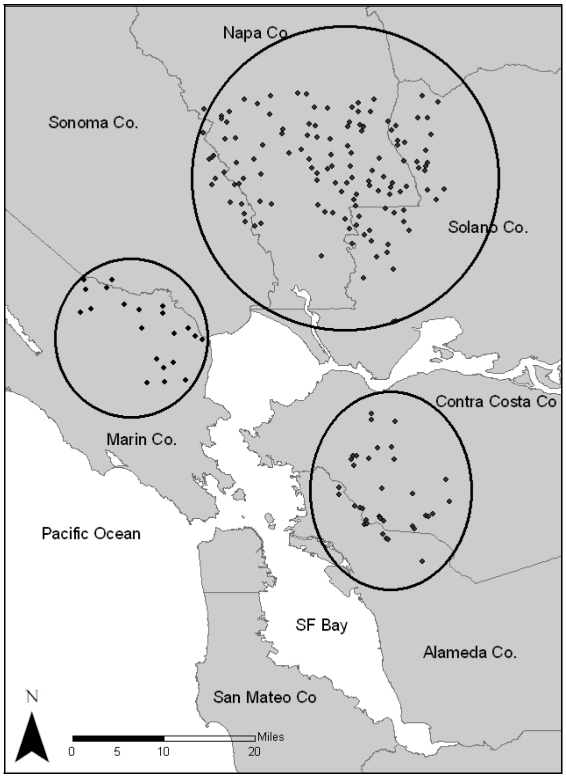

Figure 1—General locations of VTM plots selected for resampling.

The species composition and management of California's diverse oak woodlands have been subject to varied amounts of change since the arrival of European settlers. Our study area is distinct from other oak savannas and woodlands of California because of its co-dominance of coast live oak and California bay, and understory of shrubs (Allen 1990). Many native grass and forb species found in the understory of California's oak savanna have largely been replaced by introduced Mediterranean grasses and forbs across broad spatial scales within the last 250 years (McClaran and Bartolome 1988). The highly invaded oak savannas are generally considered stable communities now, and are not easily converted back to historic community types (Griffin 1977). Grasses are found in the coast live oak and California bay woodland, but this community is still dominated by woody shrubs such as toyon (*Heteromeles arbutifolia*), oceanspray (*Holodiscus discolor*), and poison oak (*Toxicodendron diversilobum*).

One of the most recently detected invasive species in California's oak woodlands is the pathogen *Phytophthora ramorum*, which causes SOD. Presumably none of the 12 plots sampled in 1933 were infected with *P. ramorum*. The symptoms of SOD were first reported in Marin County in 1994 (Svirha 1999). *P. ramorum* has led to widespread mortality in oaks and tanoaks across 14 counties in California and one county in Oregon (Rizzo and Garbelotto 2003). California bay is a foliar host and thus serves an important role in the spread of *P. ramorum*. Foliar hosts are shrub and tree species that do not die, even though *P. ramorum* may be present on leaves and branches. At the landscape level, the density of California bay is a predictor of oak mortality (Kelly and Meentemeyer 2002) presumably because infected California bay leaves produce large numbers of sporangia (Davidson and others 2005). Past research by McBride (1974) showed California bay to be the climax species in the coast live oak and California bay woodlands of the East Bay in the absence of disturbance such as livestock grazing. The ecological implications of California bay acting as the climax species and as a foliar host are important to consider in increasing our understanding of SOD disease dynamics. A future research question of ours is to determine if there are certain characteristics of historical stands that are associated with the current presence of *P. ramorum.*

In this study we: 1) evaluated the changes in basal area of primary tree species, and 2) determined tree and understory species composition change since the 1930s. Our ultimate goal is to increase our understanding of the stability of the coast live oak and California bay community as well as successional dynamics within these diverse and biologically productive woodlands.

Methods

Beginning in winter 2005, we randomly selected 12 VTM plots from a gradient of SOD infection based on previous research (Brown and Allen-Diaz 2006) in the coast live oak and California bay woodlands surrounding San Francisco Bay. Plot selection criteria were based on presence of coast live oak and California bay within the Coast Ranges of Alameda, Contra Costa, Marin, Sonoma, and Napa counties. The majority of our plots were located on north to northwest ridges between 152 and 487 m (500 and 1,600 ft). Long-term average annual precipitation ranged from 68 to 96 cm (27 to 38 inches). The plots were located across a broad spectrum of land uses, including the edge of rapidly urbanizing cities to ranches, vineyards, and wildlands and were located on both private and public land. There was no evidence of fire scarring on any of the trees measured within our plots, and only one plot was grazed by livestock.

Although the VTM plots were not permanently marked, we were confident that we sampled within 20 to 100 meters of the original plot location, based on modern GPS coordinates created through the georeferencing process (Kelly and others 2005). Plot relocation efforts were aided by original topographic maps and environmental variables, such as slope, elevation, and aspect. In addition, tree species and respective size classes improved our plot relocation efforts.

Vegetation and environmental data was recorded using the original Manual of Field Instructions for Vegetation Type Map of California protocol (see http://vtm.berkeley.edu). All original field data collection was done in English units; we provide the English units in parentheses. A rectangular plot, 40 m x 20 m (132 by 66 ft, 2 chains by 1 chain) was placed with the long axes parallel with the slope. The diameter at breast height (DBH) at 1.3 m (4.5 ft) of each tree > 10 cm (4 inches) was recorded and classified into four categories: 10 to 27.9 cm (4 to 10 inches), 28 to 58.4 cm (11 to 23 inches), 58.5 to 91.4 cm (24 to 36 inches), and 91.4 cm+ (36 inches+). Within this larger plot, a smaller plot, 40 m x 10 m, (132 x 33 ft), was arranged, and dominant understory cover was recorded for each cell, 2 m x 2 m (6 x 6 ft).

TWINSPAN (Hill 1979) analysis (n = 24) was used to determine presence and stability of coast live oak and California bay communities. Understory plants were collected in units of percent cover, while overstory trees were categorized by DBH category and converted to basal area based on the mid-point of the diameter class. Thus basal area is the metric used in the TWINSPAN matrix for trees (in m^2/ha). The data matrix was carefully examined to ensure that default cut levels of 0, 2, 5, 10, 20 were appropriate and spanned all the percent cover and DBH values contained in the species matrix. This analysis procedure follows from Allen and others (1991).

Student's t-tests were used to determine significant differences among species in community types and between sampling dates (SAS Institute 2002). A p-value of 0.05 was used as the cut-off for significance between species for each group.

Results

Thirty-six species were found in the sample plots in 2006, with very little change in species composition between the years (*table 1*). Grass is only identified to family in some of the original VTM plots, thus we are not able to evaluate the change in Poaceae between decades.

Two plant communities were identified using TWINSPAN. Group I (n = 12) was characterized by a canopy of coast live oak and California bay, and an understory dominated by *Holodiscus discolor*. Group II (n = 9) is characterized by a coast live oak and California bay overstory with a *Heteromeles arbutifolia*, California bay sapling, and grass understory. Only one plot in Alameda County shifted species composition from Group I to II, and that was based on the decrease of *Holodiscus discolor* and *Montia perfoliata* since 1933. Three plots were distinguished from the rest by the dominance of grass in the understory. One pair of plots was converted from coast live oak and California bay laurel-grass (1933) to just two oak trees with grass understory in 2006. Another plot was converted from Group I to grass, with no tree overstory remaining in 2006. The basal area of coast live oak was significantly higher in Group I, while the percent cover of California bay saplings (<10 cm DBH) was lower. *Holodiscus discolor* cover was significantly higher in Group I (*table 2*). There was no significant difference in tree basal area between 1933 and 2006 among tree species (*table 3*). However, grass cover in the understory changed in constancy from 33 percent of the plots in 1933 to 58 percent of the plots in 2006.

Table 1*—List of tree and understory species found in 1933 and 2006 with constancy values (# of plots species occurred in / total # of plots; n = 12).*

1933 tree species list	**Constancy Value**	**2006 tree species list**	**Constancy Value**
Quercus agrifolia	100%	*Quercus agrifolia*	83%
Umbellularia californica	100%	*Umbellularia californica*	83%
Arbutus menziesii	75%	*Arbutus menziesii*	50%
Quercus kelloggii	66%	*Quercus kelloggii*	50%
Quercus lobata	25%	*Quercus lobata*	25%
Acer macrophyllum	16%	*Acer macrophyllum*	8%
		Heteromeles arbutifolia	16%
Pseudotsuga menziesii	16%	*Pseudotsuga menziesii*	16%
Aesculus californica	8%	*Aesculus californica*	8%
Quercus garryana	8%	*Quercus garryana*	8%
Quercus morehus	8%	*Quercus morehus*	8%
Sequoia sempervirens	8%		
1933 understory species list		**2006 understory species list**	
Toxicodendron diversiloba	100%	*Toxicodendron diversiloba*	41%
Symphoricarpos albus	58%	*Symphoricarpus albus*	8%
Umbellularia californica	58%	*Umbellularia californica*	50%
Heteromeles arbutifolia	50%	*Heteromeles arbutifolia*	41%
Holodiscus discolor	50%	*Holodiscus discolor*	41%
Rhamnus californica	41%	*Rhamnus californica*	8%
Corylus rostrata	33%	*Corylus rostrata*	8%
Grass	33%	*Grass*	58%
Rosa californica	25%	*Rosa californica*	8%
Arbutus menziesii	25%	*Arbutus menziesii*	16%
Quercus agrifolia	16%	*Quercus agrifolia*	25%
Rubus vitifolius	16%		
Quercus kelloggii	16%	*Quercus kelloggii*	16%
Acer macrophyllum	8%		
Aesculus californica	8%		
Ceanothus sorediatus	8%	*Ceanothus sorediatus*	8%
Montia perfoliata	8%		
Polystichum munitum	8%	*Polystichum munitum*	25%
Pteris aqulina spp	8%	*Pteris aquilina* sp	8%
Quercus chrysolepsis	8%		
Quercus morehus	8%	*Quercus morehus*	8%
Sequoia sempervirens	8%		
		Mimulus aurantiacus	25%
		Arctostaphylos sp.	16%
		Baccharis pilularis	16%
		Carduus pycnocephala	16%
		Satureja douglassii	16%
		Adenostoma fasciculatum	8%
		Pseudotsuga menziesii	8%
		Stachys adjugoides	8%
		Vaccinium ovatum	8%

Table 2—*Comparison of mean basal area (m^2/ha) and percent cover of selected species occurring in Groups I and II (with standard error).*

	Basal area			**% cover**		
	Quercus agrifolia***	***Umbellularia californica***	**all tree**	***Umbellularia californica******	***Holodiscus discolor******	**all understory**
Group I	14.54 (2.28)	5.36 (1.07)	32.43 (4.54)	4.41 (1.55)	16.58 (5.46)	60.58 (7.34)
Group II	6.19 (1.56)	3.44 (0.82)	36.09 (4.15)	11.44 (2.74)	1.11 (0.99)	63.33 (5.94)

* = significant at p = 0.05

Table 3—*Comparison of basal area (m^2/ha) and percent cover for selected species between two sampling points in time (with standard error).*

	Basal area			**% cover**
	Quercus agrifolia	***Quercus kelloggii***	***Umbellularia californica***	***Umbellularia californica***
2006	8.56 (2.34)	4.33 (1.89)	6.6 (1.75)	6.5 (2.43)
1933	9.42 (2.2)	5.45 (3.11)	3.37 (0.82)	5.33 (1.77)

Discussion

Our limited sample thus far suggests that coast live oak and California bay woodlands in the Bay Area have been relatively stable over the last 70 years. In the overstory tree component, little change in basal area has occurred which is to be expected for large, long lived mature trees. Two plots had their overstory trees removed by management. One plot had a species shift from an overstory of coast live oaks with redwoods to California bay and Douglas-fir. Understory species composition has changed somewhat which is expected with shorter-lived shrub and herbaceous components. An unfortunate artifact of this historic data set is the lack of identification of the grass component to species. Detecting species composition change in the understory is also exacerbated by the original data collection method; only a single dominant understory species was recorded in each 2 x 2 m quadrat. This limits our ability to evaluate changes in biodiversity or invasive species in a plot-by-plot comparison, but does not de-value the collection for larger-scale analyses of plant community dynamics.

The coast live oak and California bay woodlands exist within the wildland urban interface where urbanization, woodland fragmentation, and introduced species will shape the composition, structure and animal communities. *P. ramorum* is one such introduced species and its affect on the successional dynamics between coast live oak and California bay are uncertain (Brown and Allen-Diaz 2006). There is evidence from this study of a modest increase in California bay saplings and mature California bay basal area since the initial sampling 70 years ago. Although it remains to be seen how California bay will respond to stand structural changes with *P. ramorum* infection, the increase in the sapling class hints at a successional trend toward California bay dominance. Historic stand characteristics that indicate resistance to *P. ramorum* infection will be equally important in understanding SOD disease dynamics.

Resampling VTM plots on both public and private land is an important tool in understanding long-term plant community change in California. However, it is important to be aware of difficulties surrounding the exact re-location of plots as well as the difficulties of sampling on private property. Re-location error based on digitized GPS coordinates can be large (Kelly and others 2005), and field samplers must use maps, topography, aspect, and mature tree stand characteristics to narrow the location of the plot. Acquiring permission to sample VTM plots on private (as well as public) lands requires finding the plot locations through the county assessor's office in order to link plots to individual land owners. We sent a letter requesting landowners' permission to allow us to sample on their property with a brief description of our project, and simultaneously UC Cooperative Extension advisors and local professionals were very helpful in assisting in contacts with individual landowners (Hilty and Merenlender 2003). Still, this process takes many, many months and resulted in approximately an 80 percent positive response.

California's population has grown from less than 7 million in the 1940s to 37 million people today, while in the Bay Area alone, ~6 million more people have come to live and work in the area's diverse ecosystems in the last 70 years (Gregor 1963). This influx of human residents has changed land use patterns, altered disturbance regimes, fragmented ecosystems and introduced countless new species into the region. The VTM collection is a plot-rich data set that offers the opportunity for examining plant community dynamics across the last 70-80 years. The collection may provide insight into the stand characteristics that resist the deadly effects of *P. ramorum* or other future invasions, while providing a valuable baseline of historic plant community data.

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Continue

Oaks Through Time: Reconstructing Historical Change in Oak Landscapes[1]

Arthur Dawson[2]

Abstract

The San Francisco Bay Area was home to some of the most celebrated valley oak lands in California, their grandeur much chronicled by early visitors and residents. Despite extensive loss, there remains substantial local interest in their preservation and restoration, necessitating an understanding of historical distribution and subsequent change. Assembling and interpreting historical and current oak data for highly modified Bay Area landscapes, such as Sonoma Valley in this study, has involved the development of a range of new techniques. The use of historical data involves many uncertainties, but through careful, site-specific integration of written accounts from the 19th century, early maps and surveys, historical landscape and aerial photographs, and modern field data, it is possible to develop a likely scenario of historical oak distribution in Sonoma Valley. This and similar studies in the Napa and Santa Clara Valleys are contributing to a detailed picture of the changes undergone by oak savannah and woodland over the last two centuries. Preliminary results indicate a highly patchy distribution within areas considered to have had relatively homogenous or continuous cover. The distribution of valley oak savannah appears to have been largely determined by microtopography, soil type, and groundwater. We have also collected age data from recently cut trees, indicating age/size relationships and suggesting that major disturbance event(s) may have occurred several decades before the arrival of Spanish and Mexican settlers. GPS-based fieldwork to identify residual heritage trees has found many more trees surviving within these modified landscapes than expected. This study has been used to assess baseline erosion rates, determine site suitability for an oak woodland mitigation project, and to assist other efforts to maintain these trees as significant components of regional landscapes into the future.

Keywords: Historical distribution, historical vegetation patterns, valley oaks.

Introduction

The earliest written description of Sonoma Valley was recorded in the journal of Father Jose Altimira during his expedition to found the Sonoma Mission in 1823 (Altimira 1823). Altimira spent several days in Sonoma Valley taking an inventory of the resources that would aid the establishment of the mission; his observations provide a substantial amount of detail about vegetation patterns at the beginning of settlement. He described a *roblar,* or white oak grove (Brown 2001), on the valley floor, with trees "very tall and robust . . . 3 leagues from east to west, and one and a half leagues from north to south, though in some parts narrower." These dimensions translate into an area approximately 7.8 miles long by 3.9 miles wide, about 30 square miles. His descriptions also include grasslands, riparian areas, uplands, and wetlands.

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[1] An abbreviated version of this paper was presented at the Sixth California Oak Symposium: Today's Challenges, Tomorrow's Opportunities, October 9-12, 2006, Rohnert Park, California.

[2] Director, Sonoma Valley Historical Ecology Program, Sonoma Valley Watershed Station, Sonoma Ecology Center, Eldridge, CA 95431. e-mail: Arthur@sonomaecologycenter.org.

In this study, I used a range of methods and sources to reconstruct the likely distribution of oaks on the floor of the Sonoma Valley at the beginning of the 19th century. By its nature, historical data contains many uncertainties and varying levels of accuracy and detail. Some sources for Sonoma Valley are quite detailed and can be easily tied to discrete points on the ground, others contain data that is less specific and more difficult to assign to definite locations. The difficulty of assessing the reliability of individual sources was addressed in several ways. Historical documents were reviewed and evaluated for content, accuracy, and location, and a field survey was carried out to map the distribution of remaining heritage oak trees. Recently collected oral histories from local elders were also consulted.

A key component of this study was the integration of this wide variety of sources, which in most cases allowed several pieces of data to be brought to bear on any particular location. This revealed converging lines of evidence among written accounts from the 19th century, early maps and surveys, historical landscape and aerial photographs, the current heritage oak survey, oral histories, soil maps, and infrastructure patterns. A similar technique was used by Cooper (1926) in reconstructing the pre-settlement characteristics of a large oak woodland near Palo Alto. The scenario of oak distribution developed in this current study should be considered a preliminary one that will be refined through further fieldwork and research.

A number of factors affect the distribution of oaks, including soil type, groundwater, micro-topography, and land use before and after European-style settlement. Of these, the effects of land use on heritage oak distribution is the most difficult to assess, and will require further study to better understand its impact. However, the results of this study suggest that a highly degraded, but discernable historical pattern can be still seen in the current distribution of heritage oaks.

Developing a picture of historical vegetation in Sonoma Valley requires taking into account the effects of land management practiced by indigenous peoples for centuries or millennia before Mexican settlement began, and was a primary consideration in the design of the study and analysis of the results (Parkman 2004). A variety of sources consistently indicate relatively open conditions at the time of settlement (Altimira 1823; General Land Office 1851-1887; O’Farrell 1848; Peabody 1851 Watkins 1888). Altimira reports Indians in the hills between Sonoma and Napa Valleys getting ready to “burn the long grass” during his visit in the summer of 1823. Other forms of native management in Sonoma Valley may have included pruning, scattering of seed, harrowing, and tilling of the soil to encourage the growth of certain plants (Anderson 2005). Details about native land management practices are outside the scope of this study, but were considered with respect to historical vegetation mapping.

Physical and historical evidence suggests that a map of pre-disturbance vegetation cover for Sonoma Valley should aim for a target date in the middle or late 18th century. However, because the earliest written records of vegetation in Sonoma Valley were not made until 1823 (Altimira 1823), reconstructing pre-disturbance conditions requires extrapolating back in time from a number of early historical sources. Building a picture of 18th-century conditions from data collected many decades or a century later would have a large potential for error. Likewise, characterizing the early to mid 19th-century landscape recorded by Altimira, Mexican land grant maps, and General Land Office (GLO) surveys as representing true pre-settlement conditions would also be inaccurate. Thus, 1800 was chosen as the middle ground between the extremes of “too early” and “too late.” The year 1800 is a date for which conditions can be reconstructed with reasonable confidence, based on historical maps, observations, and surveys collected a few decades later, as well as modern field evidence.

Methods

Age/Circumference Relationship

As a preliminary step to making a survey of heritage oaks, I tested the correlation between the age and size of valley oaks and valley oak hybrids. Ring counts and circumference measurements were taken from 18 oak stumps. Most were recently downed trees in the process of being cut up. Whenever possible, circumference measurements were made 48 inches above the base of the tree, approximately chest level when the tree was standing. Identification of species was made from remaining leaves and/or bark. In two cases for which identification was less certain, oak trees in the immediate vicinity were used as indicators.

Heritage Oak Survey

Because of their longevity, oaks provide a living record of earlier conditions. I was interested in surveying oak trees that were here at the time of the first recorded settlement of non-native people in Sonoma Valley in 1823 (Smilie 1976). When measurements from 18 valley oak stumps demonstrated a strong correlation between age and diameter (see Results), a minimum circumference of 132 inches was chosen for the heritage oak survey, corresponding to an age of about 180 years. The survey was done over the course of two weeks on foot and by car. Public roads provided physical or visual access to most parts of the valley. Where trees were visible but not accessible, conservative estimates of circumference were made. Locations of heritage trees were recorded either with a GPS unit (accuracy=30 feet), or by hand on topographical maps (accuracy = 125 feet) and transferred into a Geographic Information System (GIS) program.

Using the established age/circumference relationship (see above) valley oaks measured during the heritage oak survey were grouped into 20-year age/size classes and assigned estimated germination dates. For comparison, oaks measured during 19th-century GLO surveys (see below) were also grouped into 20-year age/size classes and assigned estimated germination dates.

Assessment and Interpretation of Historical Sources

The first step in the historical research component of this study was to assess and interpret the various data sources. Each source type required a specific approach to interpretation, taking into account how and why the data was collected, its level of detail and accuracy, vegetation changes that had already occurred, and how accurately the data could be assigned to specific points on the ground:

1. **Jose Altimira’s Journal.** With the exception of very brief mention in mission records, this document (Altimira 1823) represents the earliest written record of Sonoma Valley. Altimira traveled through the area in the summer of 1823, surveying possible sites for a new mission. His inventory of available resources, particularly vegetation, wildlife, and water, is an invaluable source of ecological data from the early 19th century. Interpreting this document presents several

challenges: it is written in archaic Spanish and thus difficult to translate (published translations are poor and contain errors); Altimira's cardinal directions are based on the position of the sun just after summer solstice and thus skewed by 30 degrees; distances are in leagues (approximately 2.6 miles) and varas (approximately 2.75 feet); and a number of landscape changes had already occurred, the most significant being the depopulation of Sonoma Valley through removal of native people to other Bay Area missions (Milliken 1995) and probably disease. My familiarity with a photocopy of the original manuscript, developed over the last six years, helped minimize these difficulties. My draft translation was checked and corrected by an expert in early California Spanish.[3] Where cross-checking is possible, Altimira's distances and other observations appear to be fairly accurate. Journal entries can be located to points within a 100-yard to 1-mile radius.

2. **Land Grant records from the U.S. Land Court.** These records primarily cover the floor of Sonoma Valley and include maps and court transcripts. Careful reading of these documents allowed comments, observations, and map features to be attributed to specific points on the ground and entered into GIS coverages (Anonymous 1837; Anonymous 1840; Anonymous 1844; Boggs 1861; O'Farrell 1848; Peabody 1851). Accuracy and detail of individual records varies considerably. Data can be located to points within a 100-yard to 1-mile radius.
3. **General Land Office (GLO) surveys.** These records primarily cover the uplands outside the boundaries of the land grants. In a few places, these surveys crossed the valley floor, allowing cross-checking of other sources. Diameters and species of bearing trees (trees marked at the intersections of township and range lines) were recorded, allowing integration with, and cross-checking of, modern field data from the heritage oak survey to develop a survivorship graph for valley oaks extending back to the late 17th century (General Land Office: 1851, 1853, 1855, 1858, 1859, 1865, 1866, 1867, 1871, 1880, 1887). These records are quite detailed and represent the most specific and accurate records from the mid-19th century. Most data can be located to points within a 100-yard radius.
4. **Historical photographs** from the late 19th century were consulted as an aid to denying or confirming vegetation types in some parts of the valley**.** Aerial photos from 1942 were also consulted for particular areas. Historical photos were carefully analyzed to identify the points from which they were taken and the features within each photograph (U.S. Department of War 1942; Watkins, 1888). Aerial photos have been used by other researchers for mapping the former distribution of oaks[4] (Brown 2001). The greatest challenge in interpreting these photos is accounting for landscape changes that had already occurred in the 65 years or more since the beginning of settlement. Data can be located to points within a 10-yard to 100-yard radius.
5. **Oral Histories:** Information recorded from local elders whose memories covered most of the 20th century were attributed to specific points and proved particularly helpful in identifying former wetlands (Dawson 2002). Accuracy is good to

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[3] Calhoun, Daniel. Personal communication. Referred by the staff at Bancroft Library, Berkeley.

[4] Grossinger, Robin; Ruygt, J. Unpublished data on file, San Francisco Estuary Institute, Oakland, CA.

excellent, and most observations can be located to points within a radius of 10 yards to 200 yards.

6. **Soil maps:** Soil maps were analyzed to determine if historical vegetation types correlated with soil type. Of particular interest were correlations between the presence of heritage oaks and soil types, and between historical wetlands and soil type. These maps were published by the Soil Conservation Service in 1972 and were based on a combination of field surveys and analysis of aerial photos from 1942. Designated soil types can be tied to points on the ground with an accuracy of 100 feet, though the "ground-truthed" accuracy of the soil boundaries themselves is unknown.

Additional Sources

Currently existing vernal pools were recorded on topographical maps and transferred to a GIS program. These pools were assumed to be relicts, indicative of former conditions in those areas. Accuracy of these locations is 125 feet.

A visual analysis using maps of existing and former infrastructure was made in certain areas to determine if there was a correlation between the presence or absence of roads and certain historical vegetation types, particularly perennial or seasonal wetlands.

A current land cover map, developed by the Sonoma Ecology Center from color aerial photos taken in 2003 as well as some fieldwork, was also consulted (Sonoma Ecology Center 2004). Land cover designations on this map include a variety of land uses, such as residential, commercial, agricultural, and park land. To test the effects of land-use on the distribution of heritage oaks, locations of trees recorded during the heritage oak survey were plotted on this map to test whether their current distribution was positively or negatively correlated with particular current land uses. The land cover map is accurate to within 100 feet.

Integration of Data Sources

Preliminary results from the heritage oak survey demonstrated that the distribution of heritage oaks was correlated with particular soil types (see Results), a phenomenon noted by Brown (2001), Griffin (1988), Cooper (1926), and Jepson (1910). Specific soil types were also found to correspond to known historical wetlands such as Tolay Lake (just outside Sonoma Valley) and the Kenwood Marsh (O'Farrell 1848; Peabody 1851; Soil Conservation Service 1972; Sonoma County Surveyors Office 1860). Given these findings, it was decided to use soil type as the starting point for developing the historical vegetation map for the floor of Sonoma Valley, and to refine it through consulting the other sources. The refinement process increased the number of polygons above those found on the soil map, resulting in a mean polygon size of about 75 acres, which can be considered a rough level of resolution for this study. The goal was to develop a map that represented likely approximations of "average" historical conditions within each polygon.

While there was significant overlap, slightly different collections of data were consulted and integrated to refine the likely extent and location of historical vegetation types. Thus, somewhat different approaches were developed for each one:

Freshwater wetlands: the former extent of seasonal and perennial freshwater wetlands was determined by an iterative refinement of the historical picture. Due to the limitations of the data, seasonal and perennial wetlands were lumped into a single category. Soil types associated with the well-documented and mapped historical wetlands of Tolay Lake and the Kenwood Marsh were marked in GIS as wetland wherever they occurred in the watershed.

Soil polygons containing currently existing vernal pools were also marked as wetland in GIS. However, as these exist on a number of soil types, some of which also contain heritage oaks, only individual soil polygons were marked in this case. The same approach was taken with wetlands documented in Altimira’s 1823 journal.

In a few cases, a polygon identified as “freshwater wetland” contained one or more heritage oaks. Depending on the number and location of these oaks, a determination was made whether to keep the “wetland” designation, change it to “oak woodland” or to divide the polygon into two or more pieces, some designated “freshwater wetland” and some “oak woodland,” (scattered oaks are sometimes found at the edges of wetlands).

Further refinements were made to the “freshwater wetland” polygons using evidence such as historical photographs, oral histories, the absence of heritage oaks, and the absence of roads, which in several cases still define the extent of historical wetland.

Oak woodlands and savannah: the likely former extent of oak woodland and savannah was determined by an iterative refinement of the historical picture. As noted above, the distribution of heritage oaks mapped during the oak survey correlated well with a limited number of soil types. These soil types were marked in GIS to develop a preliminary picture of oak distribution. To check and further refine this oak extent, a number of other sources were consulted: mid 19th-century Mexican land grant maps, mid 19th-century American maps, GLO surveys, and late 19th-century photographs. Refinement involved adjusting polygon borders and re-designating some “oak woodland” polygons as “wetland,” or “riparian forest,” where there was existing or historical evidence for the change.

To develop a rough picture of historical oak density, each soil type containing heritage oaks was scored for modern presence (number of heritage trees). The two soil types containing about one-third of the heritage trees (31 percent) received scores of 3 (high) for modern presence; the 5 soil types containing the middle third (37 percent) received scores of 2 (medium); and the 16 soil types representing the final third (32 percent) received scores of 1 (low). To avoid weighting the scores in favor of soils covering large areas, a modern density score was also calculated by dividing the area covered by each soil type by the number of heritage trees on them. The one-third of soils with the lowest density ($\geq$7.1 10^6 ft^2/heritage tree) received scores of 1 (low), the middle third (density 3.7 – 5.4 10^6 ft^2/heritage tree) were given scores of 2 (medium), and the soil types with the highest modern densities (0.2 – 2.8 10^6 ft^2/heritage tree) scored 3 (high). Finally, the modern presence and modern density scores were added to create a combined score. This combined score was applied to each polygon and used to map a possible scenario of historical oak density. As a final check, the oak distribution map was compared with the dimensions of the *roblar* described by Altimira in 1823.

Riparian forest: forested areas along creeks were considered “riparian forest.” The extent of these areas was determined by a two-step process. Soil types designated as “riverwash” were mapped in GIS as “riparian forest.” Further refinements were made using historical photographs and maps to confirm the existence and adjust the position and extent of these areas.

No evidence for oaks. Some evidence for chaparral or grassland: This category covers soil types in which no heritage trees or other evidence for historical oak presence was found, but for which there is some physical or historical evidence for chaparral or grassland. Sources for this category included Altimira's observations, GLO surveys, and modern observations.

Tidal marsh: Areas influenced by tidal flows and a mixture of salt and fresh water were identified as "tidal marsh." A coverage for tidal marsh areas as defined by the San Francisco Estuary Institute was used for this project (San Francisco Estuary Institute 1999).

Results

Age/Circumference Relation

Ring counts and measurements of 18 recently cut valley oaks and valley oak hybrids revealed a good correlation between circumference and age (*fig. 1*) for trees from approximately 80 to 280 years old. The lack of data for trees younger than this means the trendline may be in error for valley oaks less than 80 years old.

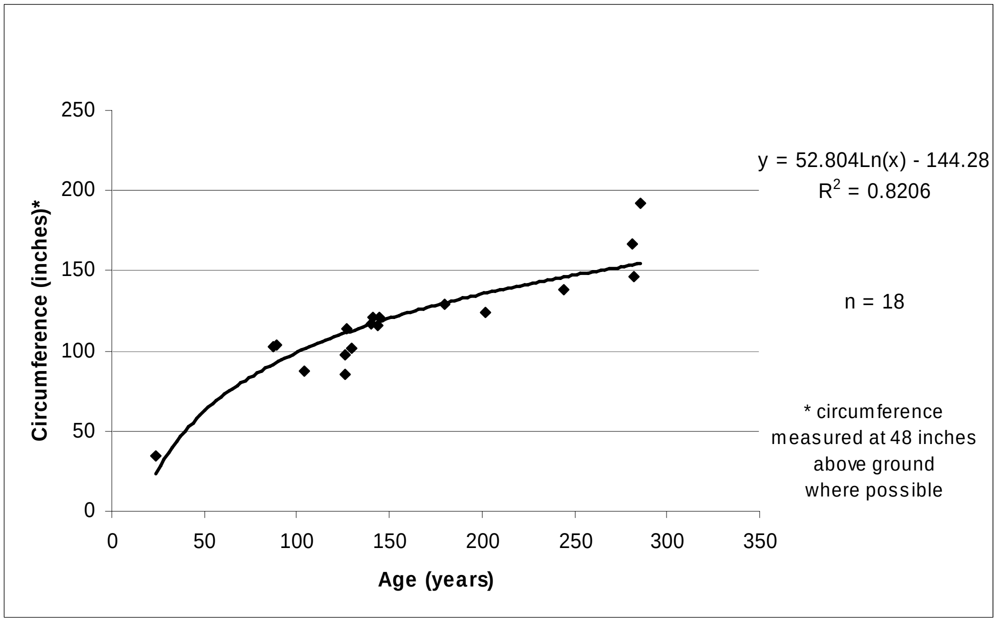


Figure 1—Valley oak age/circumference relation from ring counts of recently cut stumps, Sonoma Valley, California (includes hybrids)

Heritage Oak Survey

The heritage oak survey recorded 189 valley oak and valley oak hybrids (90 percent), 16 coastal live oaks (7.5 percent), 4 black oaks (2 percent), and 1 blue oak (0.5 percent) on the floor of Sonoma Valley with circumferences of 132 to 225 inches.

For valley oaks, this corresponds to a minimum age of 180 years, thus dating to the beginning of settlement or before. Figure 4 shows the locations of these trees.

A strong correlation was found between the presence of heritage oaks and soil type (*table 1*). Of 57 soil types found on the floor of Sonoma Valley, 23 (40 percent) had heritage oaks growing on them. Just two soil types, Tuscan cobbly clay loam and Los Robles gravelly clay loam supported approximately one-third (31 percent) of the heritage oaks, an additional five soils supported another third (37 percent), and 16 more soil types supported the remaining third (32 percent).

Heritage oaks were found growing in all land-use categories (*table 2*), with the greatest numbers in residential, commercial, and vineyard areas. Of the 23 soil types supporting heritage oaks, 21 also supported vineyards. Vineyards were found on a total of 49 soil types. Only two soil types with heritage oaks, Clough gravelly loam, and Red Hill clay loam did not have vineyards on them in 2004.

Table 1—*Soil preferences for heritage oaks, Sonoma Valley, California (includes hybrids; heritage trees defined as 132 inches or more in circumference)*

Soil type	**Slope**	**Permeability**	**# of heritage oaks**	**Modern presence** (score)	**Soil type total area** (10^6 feet^2)*	**Modern density** Square feet per tree (10^6 feet^2) (score)*	**Combined score***
Arbuckle Gravelly Loam AkB	0-5	1.31	3	Low (1)	4	1.33 (3)	4
Clear Lake Clay CeA	0-2	.13	6	Low (1)	51	8.5 (1)	2
CeB	2-5	.13	2	Low (1)	53.6	26.8 (1)	2
Clear Lake Clay Loam CcA	0-2	.13	6	Low (1)	75.3	12.6 (1)	2
Clough Gravelly Loam CgC	2-9	1.31	3	Low (1)	33.9	11.3 (1)	2
CgD	9-15	1.31	1	Low (1)	2.6	2.6 (3)	4
Goulding Clay Loam GgD	5-15	1.31	8	Low (1)	25.4	8.5 (1)	2
Huichica Loam HtA	0-2	1.31	21	Medium (2)	120.7	5.7 (2)	4
HuB ponded	0-5 ponded	1.31	1	Low(1)	2.8	2.8 (3)	**4
HtC	2-9	1.31	19	Medium (2)	102.8	5.4 (2)	4
Lariger Loam LaC	5-9	1.31	10	Medium (2)	2.1	0.2 (3)	5
Los Robles gravelly clay Loam LuA	0-5	.42	31	High (3)	42	1.4 (3)	6
LvB	0-2	.42	5	Low (1)	94.2	18.9 (1)	2
Red Hill Clay Loam RhD	2-25	1.31	13	Medium (2)	64.5	5.0 (2)	4
RhE	15-30	1.31	4	Low (1)	4.1	1.0 (3)	4
Riverwash RnA			6	Low (1)	42.8	7.1 (1)	2
Spreckles Loam SkC	2-9	.42	7	Low (1)	25.8	3.7 (2)	3
SkE	15-30	.42	6	Low (1)	22.0	3.7 (2)	3
Tuscan cobbly clay loam TuC	0-9	.42	34	High (3)	71.7	2.1 (3)	6
Wright Loam WmB	0-5	1.31	1	Low(1)	31.6	31.6 (1)	2
WgC	0-9	1.31	5	Low (1)	23.3	4.7 (2)	3
Yolo Loam YnA	0-2	1.31	3	Low (1)	13.6	4.5 (2)	3
Zamora Silt Clay Loam ZaA	0-2	.42	15	Medium (2)	61.7	4.1 (2)	4
Total Oaks			210				

*Modern presence score based on absolute number of oaks present, divided into low, medium and high categories (*see fig. 2*)
Square feet per tree score based on modern density, divided into low, medium and high categories
Total score = (modern presence score) + (square feet per tree score)
**single tree is on soil type boundary and slightly above level of former wetland

Table 2—*Locations of heritage oaks in Sonoma Valley with respect to land-use designations.*

Land-use	# Heritage oaks	% Heritage oaks
Transportation	5	2
Closed Woodland	20	9
Commercial	29	14
Vineyard	26	13
Other agriculture	13	6
Open woodland	23	11
Residential	75	36
Riparian	3	1
Urban Parks	7	3
Facilities	4	2
Grasslands	5	2
Total	210	99% (due to rounding)

The results of dividing size classes recorded during the heritage oak survey into approximate 20-year age groupings are shown in figure 3. The results of dividing size/age classes recorded in the mid 19th-century General Land Office surveys are shown in figure 4.

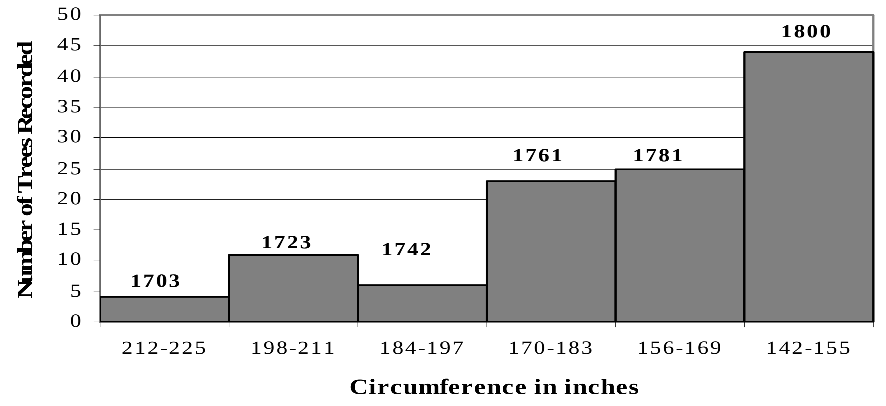


Figure 2—Valley oak size class abundance from heritage oak survey, Sonoma Valley, California (includes hybrids) (Dates are estimated germination year for middle of size class.)

Figure 3—Valley oak* size/age class abundance, Sonoma Valley, California from General Land Office surveys, 1851 to 1887 (Dates are estimated germination year for middle of size/age class.)
*recorded as "white oak"

Integration of Data Sources

Integration of all data sources resulted in figure 4. As an example of how integration worked in practice, consider an area extending about two miles from the base of the hills near Carriger Creek across the valley floor to Sonoma Creek, and north and south about two miles, including parts of present-day El Verano (*see "example area" box, fig. 4*). The heritage oak survey recorded only a few large trees in this area. Abundance scores (*table 1*) developed from the survey suggest a variety of historical conditions here, including soil types supporting very low or low densities of oaks, as well as polygons in which there was no evidence for oaks, but some evidence for grassland or chaparral. Riverwash soils along Carriger Creek define a likely riparian corridor, and the bottomlands near Sonoma Creek match soil types associated with wetlands found at former Tolay Lake and the Kenwood marsh.

I tested these designations against a number of historical sources. An early map (O'Farrell 1848) shows a few oaks in this area, with what appears to be an abundance of willows in the possible wetland area near Sonoma Creek. A Carleton Watkins photograph (1888) of the same area shows a medium density of oaks on the alluvial fan of Carriger Creek, but very scattered oaks elsewhere. Oaks can be seen in this photograph growing within the polygons designated as "no evidence for oaks." Close inspection reveals these to be relatively small trees (trunks less than 24 inches in diameter, or 72 inches in circumference) and thus most likely *not* present in 1800. The likely wetland area is too distant to be analyzed from this photo. Infrastructure analysis of the likely wetland area reveals few roads and larger parcels in this area. A street name in El Verano near Sonoma Creek is "Willow Street."

In this case, integrated analysis revealed one anomaly: a heritage oak growing in the likely wetland area. In other parts of Sonoma Valley, heritage trees were recorded in areas that have maintained their wetland character; however, these trees are all found on small mounds or rises which put them slightly above the surrounding terrain. As the polygons developed in this study are meant to represent average historical conditions, the presence of a single heritage oak in a wetland area was not deemed significant enough to change its designation, particularly given the multiple lines of evidence supporting a wetland designation.

One refinement was considered during the integration phase for this example area: raising the estimated historical oak density on the Carriger Creek alluvial fan from “low” to “medium.” As the alluvial fan does not coincide with the soil polygon for this area, it would require a substantial amount of further analysis to define this new polygon. As historical sources suggest, oak densities within this polygon ranging from “very low” to “medium” giving it an average overall value of “low.”

Discussion

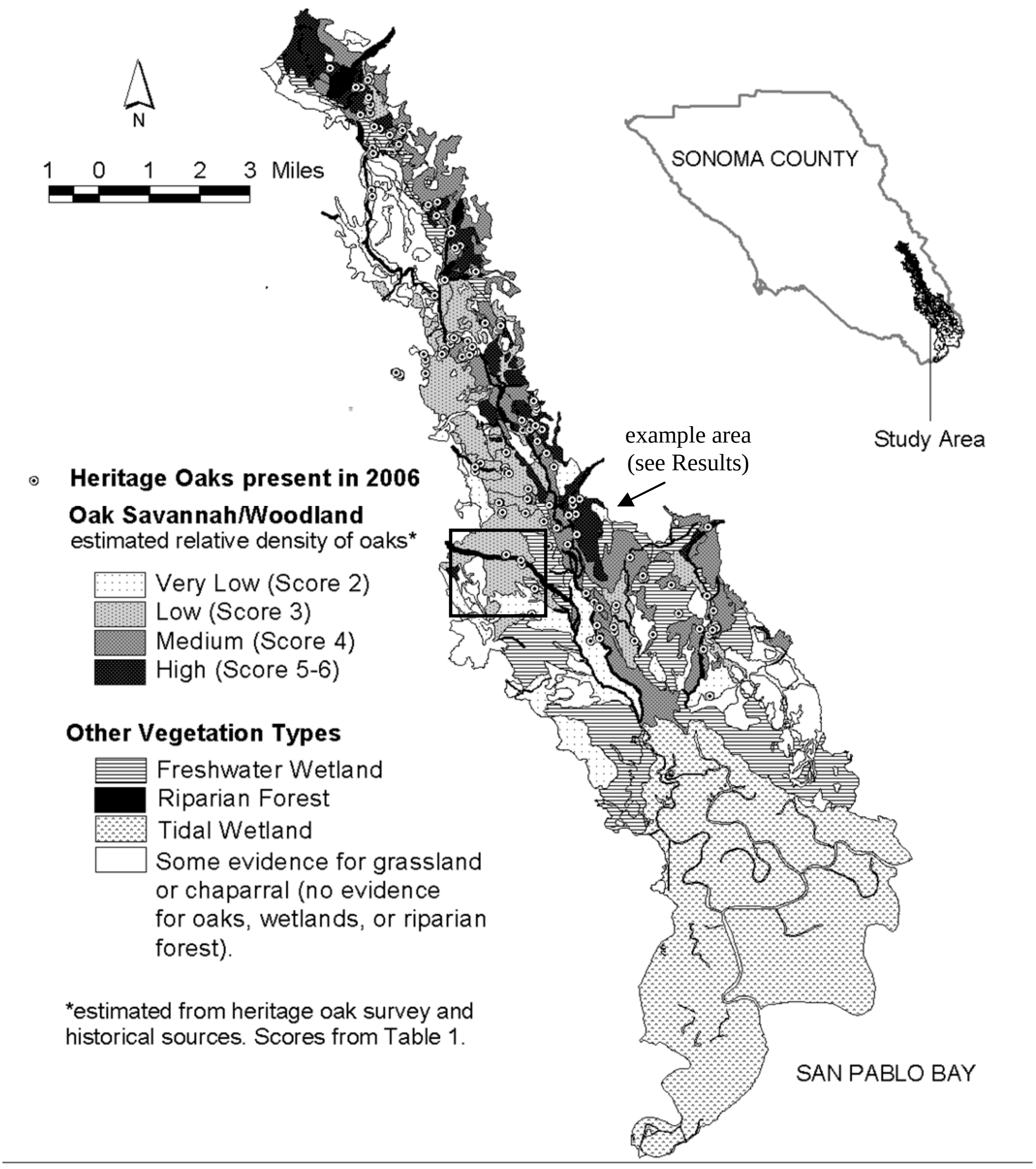
This study was able to make only a preliminary assessment of the effects of land use on heritage oak distribution. An initial analysis in table 2 shows heritage oaks growing on every land use type in Sonoma Valley. While fewer heritage oaks might be expected to survive under intensive land use designations of commercial, residential and agricultural, these were precisely where the most heritage oaks were found. Survival of heritage trees in residential areas may be due to people’s fondness for large trees, and the same may hold true, perhaps to a lesser degree, in commercial areas. Survival of heritage oaks on agricultural land is harder to explain. Perhaps agricultural lands supported a higher proportion of oaks in the past and the survivors represent a very small fraction of these original trees. If this is true, then agricultural lands are under-represented as former oak habitat. Alternately, some forms of agriculture, such as cattle raising and viticulture, may not necessarily have resulted in the clearing of large numbers of trees in the past, given the openness of the landscape depicted in early maps, accounts and photographs. Offered a choice, early settlers would likely have chosen open areas for fields and pastures. Present-day vineyards are found on 49 soil types, 21 of which also support heritage oaks. Twenty-eight soil types support vineyards but no heritage oaks; further research could determine whether some of these soils appear to offer good potential oak habitat. Another factor that was not addressed in the current study was the effect of woodcutting on the distribution of heritage oaks. While local elders report woodcutting on a commercial scale in the uplands (Dawson 2002), historical sources do not mention this activity on the valley floor.

Locations of trees recorded during the heritage oak survey suggest that small variations in microtopography played a significant role in valley oak distribution in Sonoma Valley in the past. For example, there are a number of heritage trees just east of Highway 12 in Kenwood, growing on a knoll rising about 20 feet above a former wetland. One large oak on this knoll is only 2 or 3 feet above the former wetland. Cooper (1926) mentions that groundwater at or near the surface seems to exclude valley oaks and that these trees achieve their “best development where the water table is 10 to 20 feet below the surface,” or where the roots can easily penetrate more deeply. Altimira (1823) called Sonoma Valley “a fountain of fountains” because of the abundance of surface water even in the summer. Many parts of Sonoma Valley were probably unsuitable for oaks in the past because of the high water table. Small variations in topography probably provided small areas of suitable oak habitat in places that were otherwise incompatible. For the most part, the resolution of this study was not fine enough to capture these areas.

Comparing the results of the age/size class analysis from the heritage oak survey with the age/size class analysis from the General Land Office (GLO) surveys (*figs. 2 and 3*) reveals a strikingly similar pattern, despite the fact that these data sets were collected well over 100 years apart (note: the trendline used to estimate the ages of the smaller trees recorded during the GLO surveys could be in error, as it was based on the size/age correlation demonstrated in older trees. Verification of the similarity between the heritage oak survey and the GLO surveys will require further research into the younger age classes). The most prominent aspect of both is the sudden rise in the number of surviving trees that germinated around 1800. The simplest explanation for this similarity is that both data sets reflect the same population of trees. The proportions of the various age classes did not change much over time, except that the oldest trees died off. Alternatively, an appearance of similarity could have been created by two independent factors, for example: a bias toward certain tree sizes by GLO surveyors and a greater harvesting of the 1760 and 1780 age/size class in the era immediately preceding the GLO surveys.

The distribution of oaks recorded during the heritage oak survey (*fig. 4*) matches well with the historical description of the *roblar,* taking into account the fact that Altimira did not explore beyond present-day Glen Ellen (Smilie 1975). Heritage oaks in this part of Sonoma Valley cover an area measuring 8.6 miles long by 3.9 miles at the widest, compared to Altimira's observation of 3 leagues by 1½ leagues, "though in some places narrower" (7.8 miles x 3.9 miles). Thus the distribution of heritage oaks appears to represent a highly degraded but still discernible historical pattern. Converging lines of evidence between modern field data and historical sources allowed a refinement of the historical picture to a fairly detailed level of resolution. The correlation of soil type with the presence of heritage oaks, as well as with current and former wetlands, suggests that soil type is useful as a preliminary indicator of historical vegetation. Correlation of oak presence and oak density with soil type has been noted by other researchers, including Brown (2001), Griffin (1988), Cooper (1926), and Jepson (1910). Two soil series mentioned in Brown's study, Yolo and Zamora, also occur in Sonoma Valley, with Zamora silt clay loam receiving a medium high score for heritage oak presence, and Yolo loam a medium score. Brown's historical sources for Santa Clara indicated "uneven distribution of oak woodland, oak savannah, and clearings" on these soil types. Just two soils support nearly one-third (31 percent) of the existing heritage oaks in Sonoma Valley—Tuscan cobbly clay loam and Los Robles gravelly clay loam. Brown found that a gravelly loam in the Garretson series may have supported the densest oak groves in Santa Clara. Gravelly loams cover a very small area of Sonoma Valley and support only a few heritage oaks, though the Arbuckle series has one of the highest densities of heritage oaks here.

Figure 4--Estimated Historical Vegetation, Sonoma Valley floor, c. 1800



Assume for the moment that the rise in the number of surviving oaks that germinated around 1800 is real—what would it say about the history of oaks here? The fact that this pattern shows up in both surveys suggests it is *not* just reflecting a mortality rate, with more younger oaks surviving than older ones, because the GLO surveys recorded their data from relatively young trees. In this case, the sudden rise in the oak population might be due to conditions that encouraged the survival of oak seedlings. Two possibilities are climate change, and/or a disruption in native land management such as periodic burning. California experienced a long-term drought from 1755 to 1820 (Goodridge 1991), so climate change seems an unlikely trigger for such a rise. The possibility that a decrease in native burning caused the rise in oak survival is supported by several pieces of evidence. The accumulation of leaf litter is known to favor acorn germination (Merrick and others 1999). While the first known Spanish entry into Sonoma Valley occurred in 1810, and the first settlement was established in 1823, the San Francisco mission, just 30 miles to the southwest, was established in 1775. The passage of disease along trade routes during or preceding the period of contact is well documented (Calloway 2003; Milliken 1995). The combination of missionization and disease could have severely diminished or wiped out the local native population decades ahead of settlement, potentially reducing or eliminating traditional land management practices such as burning. There are no indications in Altimira's journal (Altimira 1823) that anyone was living in Sonoma Valley at the time of his visit; in Petaluma, Napa, and Suisun he records meeting local natives, but not here. His observation of small-trunked Douglas firs on Sonoma Mountain suggests a process that can be seen today—the invasion of open grasslands by this native tree species. "Small-trunked" implies relatively young trees not more than a few decades old. As cessation (or suppression) of fire is known to encourage the growth of Douglas firs (Mac and others 1998), the disruption of native land management practices could have already left visible evidence in 1823. Further research is needed to test this hypothesis.

Conclusions

This preliminary study suggests that integrating field data and a variety of historical sources is an effective approach to developing a detailed picture of historical vegetation patterns, one that minimizes uncertainties about the accuracy of individual historical sources. This approach seems most likely to succeed in areas like Sonoma Valley where a mosaic of land uses are found and where field data on heritage oaks can still be collected. This project could probably be duplicated in other parts of the north bay, parts of the Central Valley and probably elsewhere. While broadly described as a *roblar,* the floor of Sonoma Valley at the beginning of settlement appears to have supported a complex mosaic of oak woodland, oak savannah, seasonal and perennial wetlands, riparian forest, grassland, and chaparral. Some of these historical patterns are reflected in the local infrastructure. The extent of former wetlands can still be traced in the placement of streets and roads, probably because people developed the better-drained areas first. Integrated mapping such as used in this study should prove useful as a conservation and restoration tool, identifying areas in need of preservation and places where restoration of oak landscapes is most likely to succeed. To date, the results of this study have been used to assess baseline erosion rates (through cover factor values used in modeling with the Revised Universal Soil Loss Equation), to determine site suitability for an oak woodland mitigation project being considered by the California Department of Transportation (Caltrans), and are expected to assist other efforts to maintain and restore oak woodland and other historical vegetation patterns as significant components of regional landscapes into the future.

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Continue

Applications of Growth and Survival Equations for Oregon White Oak in the Pacific Northwest[1]

Peter J. Gould,[2] Constance A. Harrington,[2] and David D. Marshall[2]

Abstract

Urban and agricultural development has greatly reduced the area of Oregon white oak (*Quercus garryana*; also known as Garry oak) woodlands and savannas in the Pacific Northwest, and much of the remainder is succeeding, or has already succeeded, to conifer-dominated forests. Conifer encroachment and, in some cases, the development of dense oak stands present significant management challenges. In this paper, new equations, now available in ORGANON, are used to predict oak growth and survival with and without management in three stands: a single-storied conifer-oak stand, a two-storied conifer-oak stand where conifers were overtopping the oaks, and a dense pure oak stand. Without conifer removal, oak basal area was projected to decline in the single-storied stand and oak mortality was projected to accelerate. Very high oak mortality (90 percent over the 50-yr projection period) was projected in the two-storied stand. Conifer removal was projected to greatly reduce mortality and increase the diameter growth of oaks in both stands. Thinning in the pure oak stand was projected to nearly triple the average diameter growth of surviving trees. The three examples indicate that management can have a dramatic effect on Oregon white oaks under stand conditions that are now common throughout the species' range.

Ke words: Garry oak, modeling, restoration, silviculture.

Introduction

Oregon white oak (*Quercus garryana*; also known as Garry oak) has the greatest latitudinal distribution of any western oak, stretching from Southern California to Vancouver Island, British Columbia (Stein 1990). Oaks are an ecologically and culturally important part of the landscape, particularly in the conifer-dominated Pacific Northwest. Many oak communities in the region are legacies of Native American land use practices, which included frequent burning to maintain prairies, savannas, and open woodlands (Sprague and Hansen 1946, Thilenius 1968). Although oaks are more widely distributed on somewhat drier sites, areas that historically supported oaks (e.g., the Willamette Valley and South Puget Sound) can typically also support conifers, particularly Douglas-fir (*Pseudotsuga menziesii*). Without fire or other repeated disturbance, oaks are often replaced by conifers, which gain a tremendous height advantage over time (Cole 1977, Foster and Shaff 2003). Succession from oaks to conifers is an on-going process in the region. Contemporary oak communities currently only cover a small fraction of their pre-settlement extent (Crawford and Hall 1997); the majority has been lost to urban and agricultural development. Some wildlife species, such as the western gray squirrel (*Sciurus griseus*, a state-listed threatened species in WA) are highly dependant on oak habitat

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[2] Research Foresters, USDA Forest Service Pacific Northwest Research Station, 3625 93rd Ave., SW, Olympia, WA 98512. e-mail: pgould@fs.fed.us.

(Ryan and Carey 1995). Thus, maintaining and restoring oak communities is a high conservation priority in the region.

Developing appropriate strategies for oak restoration depends, in part, on expected outcomes. Predictive models are useful tools for evaluating expected outcomes under different management approaches. New equations to predict the growth and survival of Oregon white oak have recently been developed and incorporated into ORGANON, an individual-tree stand-development model for forests in the Pacific Northwest (Hann 2005). The equations were developed using a larger and geographically broader dataset than those used to develop previous equations. The dataset was assembled from several sources in Oregon and southwestern Washington. Diameter growth is calculated as a function of initial tree diameter and live-crown ratio, stand basal area, and site productivity (measured using Douglas-fir site index). Survival is calculated using the same variables, except stand basal area is replaced by the basal area of trees with diameters larger than the target tree, which better reflects Oregon white oak’s intolerance to shade (Stein 1990). The new equations predict more rapid growth, but poorer survival than the equations previously used in ORGANON, which were developed using very few observations of Oregon white oak from a small portion of the species’ range. The development of the new equations is described in detail elsewhere (Gould and others in press)

In this paper, we apply the new equations to evaluate stand development with and without management intervention in three stands that represent a range of restoration challenges. Two conifer-oak stands were selected to evaluate conifer removal (or a no-action alternative) as conifers begin to overtop oaks (single-storied stand) and after oaks are already overtopped by conifers, creating a two-storied stand. A pure oak stand was selected to evaluate the use of oak thinning to accelerate the development of young stands towards a savanna structure. The three examples demonstrate the utility of the new equations and provide general insight into how management (or lack of management) is expected to affect oaks growing under different conditions.

Methods

Data from three stands were used to develop tree lists for input into a version of ORGANON that includes the new equations. Data from a conifer-oak stand located on Oregon State University’s McDonald-Dunn Forest were used for the single-storied stand. The stand had 90 ft^2/acre of basal area, with about 15 percent oak and the rest Douglas-fir. The height of the tallest oak was about equal to that of the tallest Douglas-fir, indicating that the oak had not yet become overtopped. Data for the two-storied stand were collected in a conifer-oak stand on the Fort Lewis Military Reservation in southwestern Washington. Total stand basal area was 273 ft^2/acre, with 6 percent oak and the rest Douglas-fir. Although the tallest oaks were about the same height as those in the single-storied stand (70 ft), the Douglas-fir were much taller (about 120 ft) and oaks were overtopped or in small openings. Data for the pure oak stand were also collected on Fort Lewis. The initial basal area of the pure oak stand was 123 ft^2/acre with 1,494 oaks/acre.

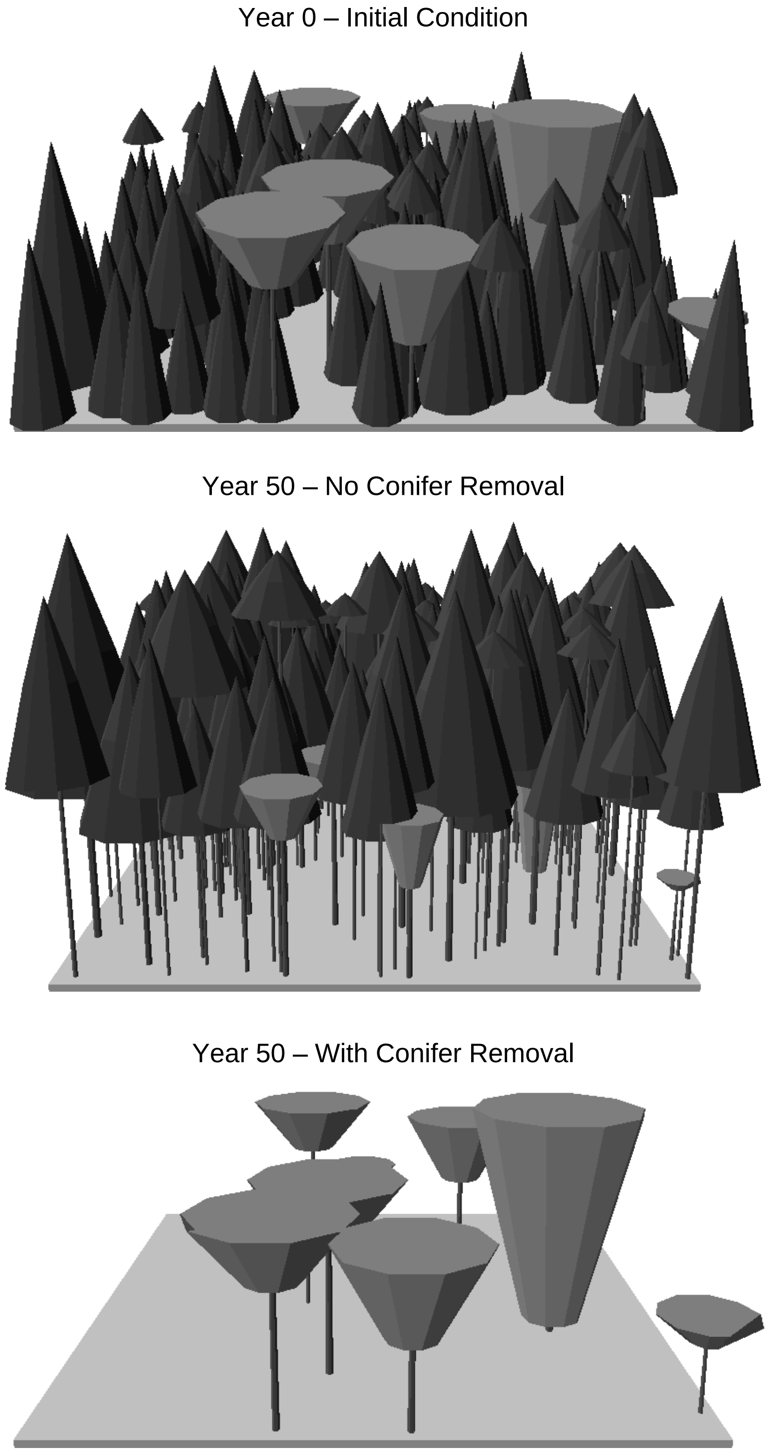
ORGANON projections were run without any management for all three stands. For the conifer-oak stands, projections were also run assuming all conifers were removed in year 0 (conifer removal). The pure oak stand was projected following thinning from below in year 0 to the approximate density of an oak savanna (30 trees/acre). The projection period was 50 yrs for all projections. Regeneration was not modeled under any of the scenarios. In addition to tables and graphs, some results were summarized using the stand visualization systems (SVS) to help illustrate projected changes in stand conditions (McGaughey 2004). Oak crown diameters in the visualizations were calculated from projected diameter at breast height (DBH).

Results

Without management intervention, the single-storied stand was projected to transition into a two-storied stand, where oaks are overtopped and mortality begins to accelerate (*fig. 1*). The Douglas-fir were predicted to outgrow the oaks by a large margin. The rate of oak mortality accelerated during the projection period; annual mortality was 0.6 percent in the first decade of the projection and 1.4 percent in the fifth decade (*table 1*). About 40 percent of oaks were ultimately projected to die. Oak basal area increased slightly in the first three decades of the projection, indicating that diameter growth initially compensated for mortality, but it began to decline in the final decades. The mean diameter growth of surviving oaks was 2.4 inches over the entire projection period.

Table 1—*Results of the ORGANON projections for the single-storied conifer-oak, two-storied conifer-oak, and pure oak stands. Number of oak trees per acre (TPA) and basal area (BA, ft^2/acre) are shown by year for the single-storied and two-storied conifer-oak stands with and without conifer removal for the pure oak stand with and without thinning.*

	Single-storied				Two-storied				Pure Oak			
	No Removal		Removal		No Removal		Removal		No Thin		Thin	
Yr	TPA	BA	TPA	BA	TPA	BA	TPA	BA	TPA	BA	TPA	BA
0	10.1	13.3	10.1	13.3	31.4	14.8	31.4	14.8	1494.0	123.3	30.0	7.6
10	9.5	13.9	9.9	15.4	19.1	10.9	29.9	17.4	1131.7	122.2	29.5	8.8
20	8.6	14.0	9.7	16.9	12.1	8.1	28.4	19.5	873.9	121.0	29.0	10.1
30	7.7	13.9	9.5	18.4	7.8	6.0	27.1	21.4	687.4	119.4	28.5	11.3
40	6.7	13.6	9.3	19.9	5.2	4.5	25.8	23.4	550.2	118.6	28.0	12.5
50	5.8	13.2	9.1	21.4	3.5	3.4	24.4	25.2	447.5	117.7	27.5	13.6



Year 0 – Initial Condition

Year 50 – No Conifer Removal

Year 50 – With Conifer Removal

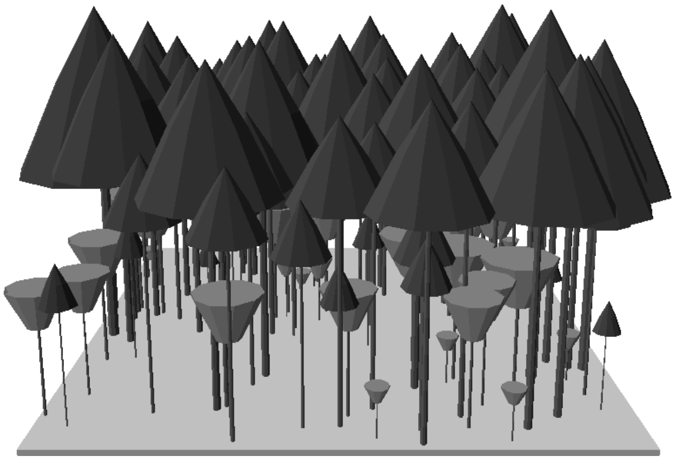
Figure 1—One-acre SVS representation of the single-storied stand in year 0 (top), year 50 without conifer removal (middle), and year 50 with conifer removal (bottom).

Oaks in the two-storied stand were already overtopped by Douglas-fir at the beginning of the projection period (*fig. 2*). Without management intervention, oaks were predicted to be nearly eliminated from the stand. Projected oak mortality was severe (*table 1*). The annual mortality rate was about 5 percent in the first decade and declined somewhat to about 4 percent in the final decade, at which point the density of oaks was already greatly reduced. In total, nearly 90 percent of oaks were expected to die during the projection period. Surviving oaks were expected to grow slowly (about 1.5 inches over the entire period) and oak basal area was projected to decline by nearly 80 percent.

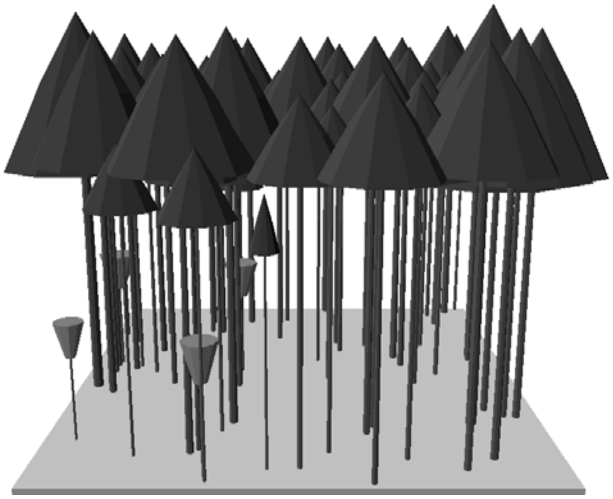
Conifer removal was predicted to have a very strong impact on oak growth and mortality in both conifer-oak stands (*table 1*). Mortality over the entire projection period was reduced to about 10 percent in the single-storied stand and to 20 percent in the two-storied stand. Oak basal area was projected to increase by 60 and 70 percent in the single-storied and two-storied stands, respectively. The mean diameter growth of surviving oaks doubled in the single-storied stand (to 4.8 inches) and more than doubled in the two-storied stand (to 4.0 inches). Both stands were projected to be oak savannas at the end of the projection period (*fig. 1 and 2*).

Without thinning, the pure oak stand was projected to experience high mortality and a small decrease in basal area (*table 1*). Stand density was projected to decrease by 70 percent and the diameter growth of surviving oaks was expected to be low, averaging 2.1 inches over the entire projection period. Thinning in year 0 greatly reduced stand density and basal area. Following thinning, the stand was projected to experience little additional mortality and the expected average diameter growth of surviving trees (6.0 inches over the projection period) was nearly three times that of the unthinned stand.

Year 0 – Initial Condition



Year 50 – No Conifer Removal



Year 50 – With Conifer Removal

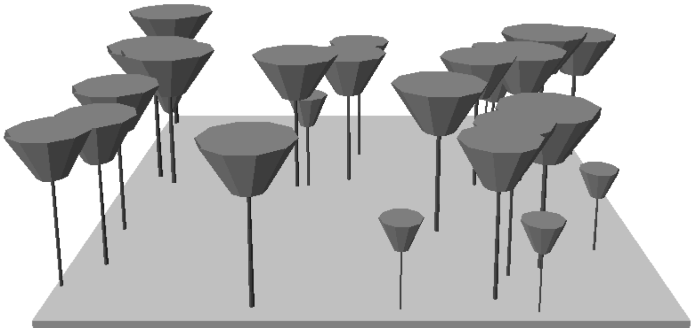


Figure 2—One-acre SVS representation of the two-storied stand in year 0 (top), year 50 without conifer removal (middle), and year 50 with conifer removal (bottom).

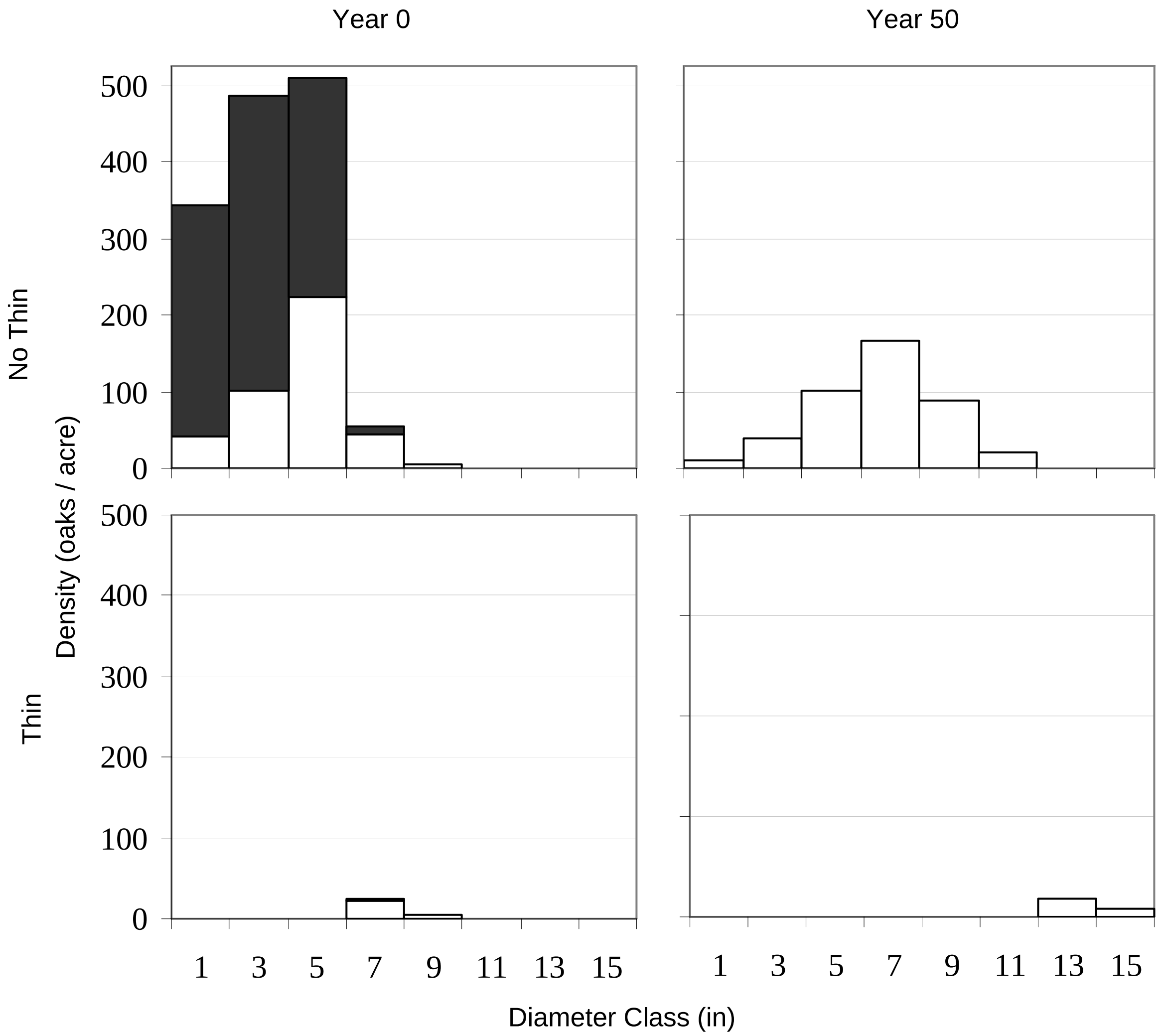
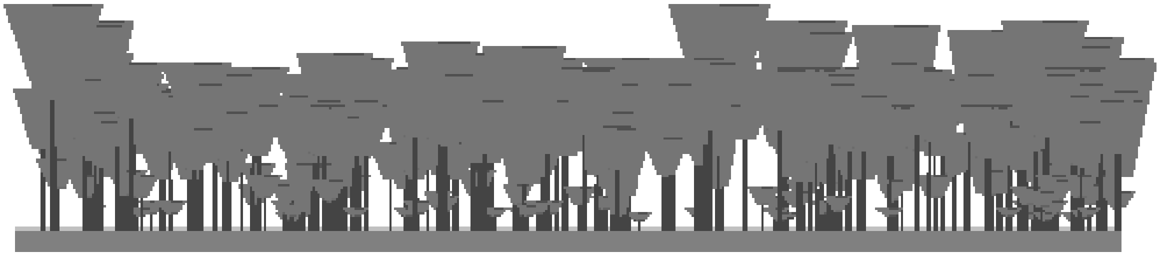


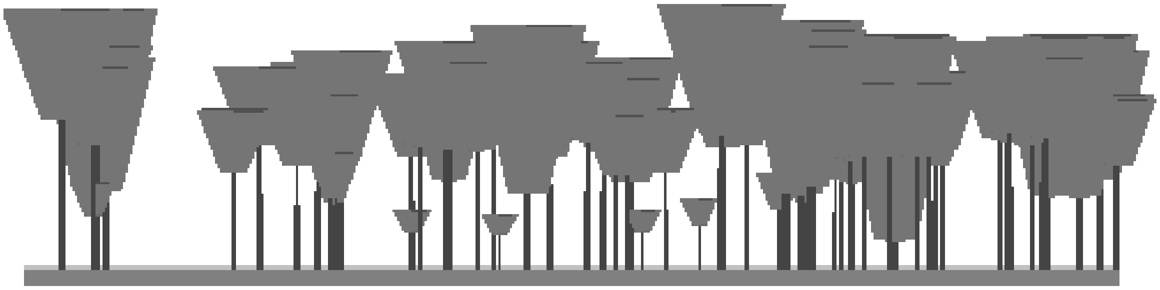
Figure 3—Initial (left) and 50-yr projected diameter distributions (right) for the pure oak stand without thinning (top) and with thinning (bottom). Black bars in the initial distributions denote expected mortality.

Without thinning, many of the small oaks in the pure oak stand were expected to die, and the mean diameter of survivors was expected to be 6.6 inches at the end of the projection period (*fig. 3*). Thinning removed nearly all the trees that were expected to die without thinning, and also many that were expected to survive. All of the residual oaks in the thinned stand were expected to be > 12 inches DBH at the end of the projection period (mean diameter 13.6 inches). Stand visualizations illustrate the more rapid development of oaks following thinning compared with the scenario without thinning (*fig. 4*).

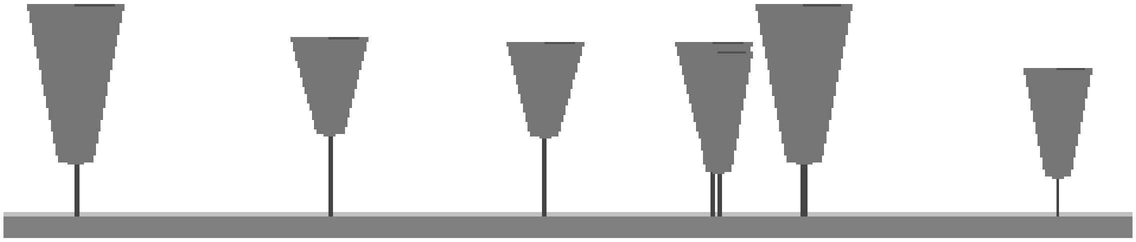
Year 0 – No Thinning



Year 50- No Thinning



Year 0 – Thinned



Year 50- Thinned

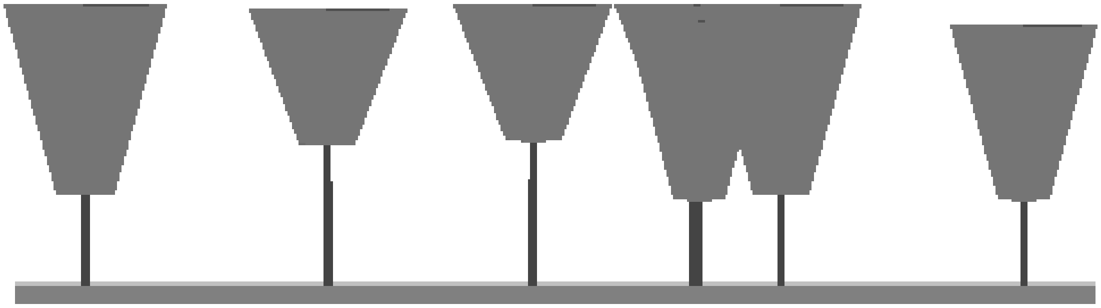


Figure 4—SVS profile view of the pure oak stand in year 0 and year 50 with and without thinning. Profiles represent an area 208 ft long and 40 ft wide.

Discussion

The conifer-oak stands represent different stages of the on-going process of succession from oak to conifers. The single-storied stand appeared to be near the tipping point where oak mortality would begin to accelerate and reduce oak basal area. Predicted mortality in the two-storied stand was severe beginning in the first decade of the projection. Most conifer stands are thinned about every 10 years on Fort Lewis, which may have allowed oaks to persist up to the present in the two-storied stand. However, the examples presented here suggest that competition with conifers becomes more severe over time. Periodic thinning may become less effective as the difference in size between oaks and conifers increases and the vigor of surviving oaks declines. Even under favorable conditions (e.g., after complete conifer removal), released oaks are expected to grow fairly slowly as they often have low crown ratios. The loss of oaks can significantly reduce the restoration potential of a stand as a great deal of time is required to replace them. Our results suggest that oaks will respond to release even in a later stage of conifer succession, but earlier intervention is needed to prevent oak mortality. The need for management intervention becomes much more urgent as succession continues and the density and vigor of surviving oaks decline.

The density of oaks, much like that of conifers, has increased in some areas following fire suppression and other changes in land use (Gedalof and others 2006, Tveten and Fonda 1999). Thinning oak stands should appreciably accelerate the development of large trees and help to maintain the more open character of historic oak woodlands and savannas. The question of how much thinning is appropriate will depend on the particular objectives of the project. Based on oak’s shade intolerance and the potential for two-sided competition for water during dry summers (Kelty and others 1987), it may be desirable to maintain low stand densities through some combination of thinning and prescribed fire. Mixed-hardwood stands where oaks are overtopped or compete with non-oaks in the upper canopy may also benefit from some combination of release and thinning treatment.

Additional factors that are not considered in the ORGANON model can also affect oak development. Some mechanical damage is likely to occur during release or thinning operations. Extensive damage may reduce oak growth and survival relative to the model predictions since such treatment impacts are not specifically considered in the model. ORGANON estimates the effects of competition at the stand level, which does not consider the spatial arrangement of trees. Conifer removal within the vicinity of individual oaks may be as beneficial as stand-wide removal in some cases. The best approach in such cases may be to collect data only within the vicinity of oaks and use ORGANON to model the portion of the stand that is likely to be treated.

Predictive models are useful tools for evaluating the effects of alternative management strategies. The new equations for Oregon white oak, which are based on considerably more information than previous ones, can give users greater confidence in ORGANON’s projections. The stand conditions evaluated here represent some of the challenges faced by land managers. ORGANON can be used to evaluate specific stands and, if needed, to tailor more complex prescriptions.

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Continue

Posters

Continue

State and Transition Models for California's Sierra Nevada Foothill Oak-Woodlands[1]

Melvin George,[2] Neil McDougald,[3] Dennis Dudley,[4] Larry Forero,[5] Bill Frost,[6] Jim Sullins,[7] and Roger Ingram[8]

Abstract

University of California Cooperative Extension and USDA Natural Resources Conservation Service are developing ecological site descriptions for the oak-woodlands in Major Land Resource Area 18 (Sierra Nevada foothills). Vegetation surveys conducted during the spring and summer of 2004 and 2005 determined woody plant canopy cover and density, and understory cover, production and species composition. Data from these surveys and soils data from SSURGO are being used to delineate sites based on woody plant species composition, understory productivity, soil texture, soil depth and precipitation. Extensive areas of oak woodlands in the central Sierra Nevada foothills are on soils (Ahwahnee, Vista and Auberry) developed from granitic parent material and will be grouped into a single ecological site. This site is dominated by blue oak (*Quercus douglasii*), interior live oak (*Q. wislizeni*), foothill pine (*Pinus sabiniana*), wedgeleaf ceanothus (*Ceanothus cuneatus*), manzanita (*Arctostaphylos* spp.), and poison oak (*Toxicodendron diversiloba*). Dominant species in each ecological site are being incorporated into vegetation state and transition models that will illustrate dynamics of the long-lived tree and shrub layers in response to fire and vegetation management.

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[1] This paper summarizes a poster that was presented at the Sixth California Oak Symposium: Today's Challenges, Tomorrow's Opportunities, October 9-12, 2006, Rohnert Park, California.

[2] Specialist,University of California, Davis, Dept. of Plant Sciences One Shields Avenue 1210 Plant and Environmental Sciences Bldg Davis, CA 95616-8780, email: mrgeorge@ucdavis.edu.

[3] County Director/Farm Advisor, University of California Cooperative Extension, Madera County 328 Madera Avenue Cooperative Extension Madera County Madera, CA 93637. e-mail: nmcdougald@ucdavis.edu.

[4] Rangeland Management Specialist, USDA Natural Resources Conservation Service. e-mail: dennis.dudley@ca.usda.gov.

[5] Farm Advisor, University of California Cooperative Extension, Shasta County 1851 Hartnell Avenue Redding, CA 96002. e-mail: lcforero@ucdavis.edu.

[6] County Director/Natural Resource Advisor, University of California Cooperative Extension, El Dorado County 311 Fair Lane Placerville, CA 95667. e-mail: wefrost@ucdavis.edu.

[7] County Director, University of California Cooperative Extension, Tulare County 4437-B S. Laspina St. Tulare, CA 93274. e-mail: cdtulare@ucdavis.edu.

[8] Farm Advisor, University of California Cooperative Extension, Placer-Nevada Counties 11477 E Avenue Auburn, CA 95603. e-mail: rsingram@ucdavis.edu.

Rangeland Health Criteria for California's Oak Woodlands[1]

Melvin George[2] and Jon Gustafson[3]

Abstract

The 17 rangeland health criteria developed by USDA and USDI are each important in one or more rangeland ecosystems. In the oak-woodlands of California some of the 17 criteria such as rills, bare ground, gullies, litter amount and movement, functional/structural groups, plant mortality/decadence, and reproductive capability of perennial plants should be important indicators of soil/site stability, hydrologic function and biotic integrity on most ecological sites. Some parameters, such as waterflow patterns, pedestals/terracettes, wind scouring, soil surface resistance to erosion, soil surface loss or degradation, and plant community composition and distribution relative to infiltration and runoff will only be important indicators on some sites in the oak woodlands.

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[1] This paper summarizes a poster that was presented at the Sixth California Oak Symposium: Today's' Challenges, Tomorrow's Opportunities, October 9-12, 2006, Rohnert Park, California.

[2] Specialist, University of California, Davis, Dept. of Plant Sciences One Shields Avenue 1210 Plant and Environmental Sciences Bldg Davis, CA 95616-8780. e-mail: mrgeorge@ucdavis.edu.

[3] Rangeland Management Specialist, USDA Natural Resources Conservation Service. e-mail: jon.gustafson@cs.usda.gov.

Black Oak-Pine Habitat Enhancement on the Lassen National Forest[1]

Mark Williams,[2] Coye Robbins,[3] and Ryan Burnett[4]

Abstract

The composition and structure of western North American forests have been altered by fire-suppression, timber harvest, and perhaps climate change. In the Sierra Nevada Mountains of California, these factors have tipped the competitive balance in favor of shade tolerant conifers over shade intolerant pines and hardwoods. California black oak, a shade intolerant species, is particularly susceptible to encroachment of conifers in the disturbance limited ecological condition that exists. Thus, without management intervention, the health, extent, and eventually the long-term viability of the pine-black oak forest is threatened. In 2005, a pilot project was implemented to curb the decline and potential loss of black oak and other hardwoods and enhance wildlife habitat value on approximately 1000 acres of mixed conifer hardwood habitat in the Almanor Ranger District of the Lassen National Forest. Objectives of this project were to increase oak canopy and pine dominance, enhance shrubs and herbaceous understory, and reduce fuels to allow for future use of prescribed fire. As pine hardwood restoration is a relatively new management practice within higher elevation conifer/oak woodlands, monitoring and an adaptive management strategy were implemented in order to provide forest managers with scientific results to help guide future projects. Vegetation monitoring was implemented to investigate changes in stand composition and structure from the canopy to the forest floor as well as oak regeneration and growth. Point count stations for censusing breeding birds were established in all treated and adjacent reference stands. Land bird monitoring will provide information on a suite of species that occupy a wide range of niches within pine-hardwood habitat; allowing for a more ecologically based approach to pine-oak enhancement.

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[1] This paper summarizes a poster that was presented at the Sixth California Oak Symposium: Today's' Challenges, Tomorrow's Opportunities, October 9-12, 2006, Rohnert Park, California.

2 Wildlife Biologist, USDA Forest Service, Region 5, Lassen National Forest, Almanor Ranger District, email: mrwilliams02@fs.fed.us.

3 Wildlife Biologist, USDA Forest Service, Region 5, Lassen National Forest, Almanor Ranger District, email: crobbins@fs.fed.us.

[4] Program Leader, PRBO Conservation Services, email: rburnett@prbo.org.

An Assessment of Sudden Oak Death in California: Current Status and Trends[1]

Lisa Fischer,[2] Jeff Mai,[3] Zach Heath,[4] and Erik Haunreiter[5]

Abstract

Aerial surveys covering 23 counties in California were conducted in 2005 to map current host tree mortality and subsequently target ground-based sampling for early detection of *Phytophthora ramorum,* the cause of Sudden Oak Death. The intent of this survey was twofold: 1) to document mortality that has spread from areas within known infested counties not mapped for several years, and 2) to continue efforts to detect *P. ramorum* within relatively high risk, currently uninfested host habitats. This assessment will discuss 2005 accomplishments and look at how the disease has spread since our surveys began in 2001. Approximately 81,000 acres of hardwood mortality were mapped. Mapped oak mortality occurs primarily on private land, with a small percentage on US Forest Service and state land. To improve the efficiency of the ground-based sampling, polygons mapped as oak mortality were stratified by risk of establishment and spread of Sudden Oak Death as determined by Meentemeyer et al. (2004). Targeted ground surveys covered seven California counties with four new findings in Humboldt County expanding the known infested area into two watersheds. Although at present SOD remains undetected in Del Norte or San Luis Obispo counties, these counties, as well as several other coastal counties have significant land area at high risk for future infestation, with the majority of this under private ownership. Trends in mortality and SOD confirmations by host type suggest that vegetation types containing coast live oak have less mortality and fewer confirmations of SOD while those with a tan oak component appear to be increasing both in terms of mortality area and new confirmations. A more collaborative approach will be emphasized in 2006 by increasing efforts to coordinate our aerial and ground surveys with other monitoring and detection efforts.

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[2] Program Manager, USDA Forest Service, Region 5, Regional Office, Remote Sensing Lab. e-mail: lisafischer@fs.fed.us.

[3] National Aerial Survey and Aviation Safety Manager, USDA Forest Service, National Aerial Survey and Aviation Safety Manager. e-mail: jmai@fs.fed.us.

[4] Aerial Survey Specialist, USDA Forest Service, Region 5, Regional Office, Remote Sensing Lab. e-mail: zheath@fs.fed.us.

[5] GIS Analyst, USDA Forest Service, Region 5, Shasta-Trinity National Forest, McCloud Ranger District. e-mail: ehaunreiter@fs.fed.us.

Effects of Prescribed Fire on Soil Properties in Oak Woodlands[1]

Alexandre Swarowsky,[2] Anthony O'Geen,[3] David Lewis,[4] Ken Tate,[5] and Randy Dahlgren[6]

Abstract

A large proportion of the State's surface water passes through oak woodlands as direct rainfall or snow melt from higher elevations. Oak woodlands are used extensively for cattle grazing, providing approximately 75% of the forage produced on California's rangelands. Vegetation management is needed in these landscapes to maintain open space, reduce fuel loads, and manage weed infestations. Prescribed fire is an effective vegetation management tool. Recently there has been a great deal of concern regarding the impacts of rangeland management on water quality. Transport of water quality contaminants to surface water bodies are of concern. The project objective is to document the effects of prescribed fire on biogeochemical properties of oak woodland soils. Prescribed fire treatments were completed in two oak woodland watersheds at UC Hopland and Sierra Foothill research and extension centers. The top 3-cm of soil was sampled before and after burning for nutrient analysis. Biomass was collected before the burn. Soil organic carbon did not change after prescribed fire and nitrogen increased. Under oak, 32% of biomass-N was supplied to soil after burning, corresponding to 20.2 kg ha-1 increase. The remaining 68% of biomass-N was lost through volatilization. In open grass, 34% of biomass-N was supplied to soil after burning, corresponding to a 14.6 kg ha-1 increase. The N returned to soil after fire was low, less than the amount supplied as manure at stocking rates of 3 cows per hectare. Phosphorus has higher volatilization temperatures (>500 C) compared to nitrogen (200 C), thus the relative amount of P returned to soil after burning was higher. Results suggest that prescribed fire will not increase nutrient supply to streams since very little N was released. This is likely the case for P because its mobility is limited in soil, however, transport by accelerated erosion may be amplified by fire.

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[2] University of California, Davis, Soils and Biogeochemistry Graduate Group, One Shields Avenue, Davis, CA 95616. e-mail: aswarowsky@ucdavis.edu.

[3] Soil Resource Specialist, University of California, Davis, Cooperative Extension Department of Land, Air and Water Resources. e-mail: atogeen@ucdavis.edu.

[4] Watershed Management Advisor, University of California Cooperative Extension, Sonoma County, 133 Aviation Boulevard, Suite 109 Santa Rosa, CA 95493. e-mail: djllewis@ucdavis.edu.

[5] Rangeland Watershed Specialist, University of California, Davis Department of Plant Sciences One Shields Avenue 1210 Plant and Environmental Sciences Bldg Davis, CA 95616-8780. e-mail: kwtate@ucdavis.edu.

[6] Professor, Pedologist, Soil Mineralogist-AES, University of California, Davis Soils & Biogeochemistry Program 3134 Plant and Environmental Sciences Building Davis, CA 95616. e-mail: radahlgren@ucdavis.edu.

Residual Dry Matter (RDM) Disappearance on Hardwood Rangeland[1]

William Frost,[2] Kenneth Churches,[3] and James Bartolome[4]

Abstract

Residual dry matter (RDM) is a standard used by grassland managers for assessing the level of grazing use on annual grasslands and associated savannas and woodlands. It indicates the combined effects of the previous season's forage production and its consumption by grazing animals of all types. The standard assumes that the amount of RDM remaining in the fall, subject to site conditions and variations in weather, will influence subsequent species composition and forage production, in addition to providing soil protection and protecting against nutrient losses. While RDM is measured at the beginning of a new growing season, grazing does not always occur continuously up to this time. Managers do not have information to predict the disappearance of residual dry matter due to physical and chemical breakdown during a period of non-grazing. In this study we investigated the rate of RDM disappearance during the summer (non-growing) period on hardwood rangeland. Our results demonstrate that the amount residual dry matter, by weight, will average a decrease of 7% per 30 day period from the time of peak standing crop of annual herbaceous species to occurrence of the germinating fall rain. The time of peak standing crop is generally accepted to be the time at which the vast majority of annual species cease growth. With the information from this study, grassland managers will be able to determine the amount of herbaceous material that must be left at peak standing crop to insure adequate amounts of residual dry matter at the time of the first fall rains to provide for site protection. Thus, management of grazing animals can be altered to optimize the utilization of annual herbaceous production while maintaining the residual dry matter to provide site protection and insure long-term productivity.

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[2] Natural Resource Advisor/County Director, University of California Cooperative Extension, El Dorado County 311 Fair Lane Placerville, CA 95667. e-mail: wefrost@ucdavis.edu.

[3] Farm Advisor Calaveras County Director 4-HYD Advisor, University of California Cooperative Extension, Calaveras County, Government Center 891 Mountain Ranch Road San Andreas, CA 95249. e-mail: cdcalaveras@ucdavis.edu.

[4] Professor of Environmental Science, Policy and Management (ESPM) University of California, Berkeley, Department of Environmental Science, Policy and Management 137 Mulford Hall Berkeley, CA 94720-3114. e-mail: jwbart@nature.berkeley.edu.

Riparian Revegetation Outcomes on California North Coastal Ranches[1]

Michael Lennox,[2] David Lewis,[3] Ken Tate,[4] Randy Jackson,[5] Stephanie Larson,[6] John Harper,[7] and Robert Katz[8]

Abstract

We are researching revegetation effectiveness and restoration trajectory of riparian habitat in coastal California. Our poster compares species specific results and vegetation groups using preliminary results from 102 sites surveyed in a cross-sectional post project analysis. Project sites of various ages have been characterized to compare site outcomes given the original methods of restoration utilized. Project sites selected were tributary stream corridors in Marin, Sonoma, and Mendocino Counties ranging from 4 to 40 years since revegetation was initiated. Oak woodland management has utilized riparian corridors for conservation and restoration. However, what is the long-term fate of these efforts and how do sites change over time? Preliminary results show the importance of collecting specific environmental data to assist the interpretation of a population response to management. Plot scale results show effects of revegetation method by landform class, or similar geomorphic features. For example, planted sites have greater density of juvenile oak trees than non-planted sites for the upper bank landform compared to floodplain plots. Successful oak establishment at planted sites on the upper bank landform is confirmed by an increase over time of both juvenile oak tree density and oak canopy cover. Incorporating time into our analysis offers adaptive management feedback and greater statistical power for understanding the effects of project design and maintenance on project performance. Validating desired outcomes and measuring unanticipated results is important for conserving California's oak populations. Our results indicate an increase in exotic cover over time. Vegetation management may be considered to ensure both weed management and broad participation in restoration efforts from watershed landowners. Specifically, how to reintroduce disturbance to riparian sites as a tool for optimizing floristic diversity while maintaining habitat value? This research project is a collaborative effort between resource agencies, consultants, private landowners, academics, and watershed groups working in north coastal California.

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[2] Staff Research Assistant, University of California Cooperative Extension, Sonoma County 133 Aviation Boulevard Suite 109 Santa Rosa, CA 95403-2894. e-mail: mlennox@ucdavis.edu.

[3] Watershed Management Advisor, University of California Cooperative Extension, Sonoma County, 133 Aviation Boulevard, Suite 109 Santa Rosa, CA 95493. e-mail: djllewis@ucdavis.edu.

[4] Rangeland Watershed Specialist, University of California, Davis Department of Plant Sciences One Shields Avenue 1210 Plant and Environmental Sciences Bldg Davis, CA 95616-8780. e-mail: kwtate@ucdavis.edu.

[5] Assistant Professor, University of Wisconsin, Madison 463 Horticulture-Moore Hall-Plant Sciences 1575 Linden Dr Madison, WI 53706. e-mail: rdjackson@wisc.edu.

[6] Livestock, Range Management Advisor, University of California Cooperative Extension Sonoma County, Sonoma County 133 Aviation Boulevard Suite 109 Santa Rosa, CA 95403-2894. e-mail: slarson@ucdavis.edu.

[7] Mendocino County Director and Livestock & Natural Resources Advisor, University of California Cooperative Extension, Mendocino County 890 N. Bush Street Ukiah, CA 95482. e-mail: jmharper@ucdavis.edu.

[8] UC Cooperative Extension.

Biologically-Based Means for Control of Oomycete Phytopathogens[1]

Michael Cohen,[2] Emiko Condeso,[3] Brian Anacker,[4] Nathan Rank,[5] and Mark Mazzola[6]

Abstract

We are investigating control of *Pythium* and *Phytophthora* spp. by zoospore-lysing bacteria, hyphae-consuming amoebae, and glucosinolate-containing seed meal. The bacterium *Pseudomonas fluorescens* strain SS101, which releases a surfactant that disrupts zoospore membranes, reduces infections by *Pythium* spp. in hydroponic plant culture (Appl. Environ. Microbiol. 69:7161, 2003). Detached leaves or seedlings of *Laurus nobilis* and *Umbellularia californica*, and seedlings of *Lithocarpus densiflorus* were sprayed with strain SS101 cell suspensions. In detached leaves inoculated with *P. ramorum* sporangia suspensions, efficacy of SS101 was highly variable with results ranging from 97% reduction in infection frequency to no significant reduction relative to the control. This finding may be due to variation in the proportion of sporangia that directly germinate into hyphae. The bacterial treatment conferred no apparent protection to seedlings placed in the understory of *P. ramorum*-infested *U. californica* trees during the rainy season. Current studies on foliar disease control are focusing on amoebae, isolated from *P. ramorum*-infection lesions of *U. californica* leaves, that exhibit hyphal feeding activity. For soil assays, cells of strain SS101 were inoculated into orchard soil, with concomitant addition of soy flour to stimulate amplification of resident *Pythium* spp. populations, and wheat seeds were sown. SS101 application resulted in substantial reductions in *Pythium* spp. root infection frequency and culturable *Pythium* spp. *propagules* in soil relative to the nontreated control. Incorporation of 0.5% (vol/vol) *Brassica juncea* var. Pacific Gold seed meal, which releases inhibitory 2-propenyl isothiocyanate, resulted in dramatic long-term reductions in culturable oomycetes in soils and prevented *Pythium* spp. infection of apple seedlings planted into the treated soil. We are presently testing the effectiveness of SS101 and seed meal treatments for the capacity to control other oomycetes, including soil-borne *P. ramorum*. Further development of biologically-based treatments may prove valuable for eliminating *P. ramorum* infestations in nurseries and ameliorating disease severity in landscapes.

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[2] Assistant Professor of Biology, California State University, Sonoma. e-mail: cohenm@sonoma.edu

[3] Sonoma State University, Department of Biology.

[4] Graduate Student, University of California, Davis. e-mail: brian.anacker@ucdavis.edu

[5] Professor of Biology & Director of Fairfield Osborn Preserve, California State University, Sonoma. e-mail: rank@sonoma.edu.

[6] Research Plant Pathologist, USDA-Agricultural Research Service, Tree Fruit Research Laboratory. e-mail: mazzola@tfrl.ars.usda.gov.

Objective Ordination and Practical Classification of California Hardwood Rangelands[1]

Emilio A. Laca,[2] Maximo Alonso,[3] Melvin George,[4] and Craig Schriefer[5]

Abstract

We sampled 457 100-m transects in California hardwood rangelands from Shasta to Ventura Counties, both in the Coastal and Sierra Foothill areas in the growing seasons of 2004 and 2005. The number of times the vertical canopy projection of each woody species was intercepted was used as a measure of composition. Woody plant densities were also described by distance to nearest tree, and herbaceous botanical composition was estimated using the species rank method. The goal of this work was to use ordination methods to organize and summarize the composition of woody plants, and to determine if objective groups or types of vegetation composition could be identified. Of the 457 transects, 260 intercepted woody plants. Data were analyzed by principal coordinate analysis and non-metric multidimensional scaling (NMDS). As expected, NMDS performed better. Stress equaled 10.8 for NMDS with 4 axes, and the correlations between original distance (manhattan) based on all 56 woody species and distance based on 2 and 3 axes were 0.87 and 0.93. Thus, ordination was successful. All transects with *Quercus agrifolia* were clearly separated from those with *Q. douglasii* and/or *Q. wislizeni* by the first axis. Based on all four ordination axes, no obvious discontinuous groups were present, but the scatter was well summarized with 10-15 groups. We conclude that non-metric scaling is a good method that can yield better, more objective ordination of hardwood rangelands. NMDS and correspondence analyses are further explored to determine if an improved, practical classification of California hardwood rangelands can be obtained.

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[2] Assistant Professor, University of California, Davis, Department of Plant Sciences One Shields Avenue 1210 Plant and Environmental Sciences Bldg Davis, CA 95616-8780. e-mail: ealaca@ucdavis.edu.

[3] Graduate Student, University of California, Davis, Department of Plant Sciences One Shields Avenue 1210 Plant and Environmental Sciences Bldg Davis, CA 95616-8780. e-mail: malonso@ucdavis.edu.

[4] Specialist, University of California, Davis, Dept. of Plant Sciences One Shields Avenue 1210 Plant and Environmental Sciences Bldg Davis, CA 95616-8780. e-mail: mrgeorge@ucdavis.edu.

[5] Lab Assistant, University of California, Davis, Department of Plant Sciences One Shields Avenue 1210 Plant and Environmental Sciences Bldg Davis, CA 95616-8780. e-mail: cschriefer@ucdavis.edu.

Grazing Impacts on Water Quality of California Oak Woodland Watersheds[1]

Kenneth Tate,[2] Randy Dahlgren,[3] E. Rob Atwill,[4] David Lewis,[5] John Harper,[6] and Barbara Allen-Diaz[7]

Abstract

Oak woodland-annual rangelands occupy three million hectares in California, and represent the landscape where California's urban-wildland-agricultural interface is most pronounced. Grazing and prescribed fire are the most cost effective vegetation management tools available to most rangeland managers. The objective of this study was to use a paired watershed design to determine the watershed scale effects of grazing intensity on water quality, hydrology, nutrient cycling and plant community dynamics on annual rangelands. We used the small watershed (<200 acres) as our experimental unit as management occurs on the small watershed scale making the results of this study directly applicable to managers. Following four years of pre-treatment calibration, we applied the following treatments at research stations in both the Sierra Nevada foothills and Coast Ranges: i) non-managed reference, ii) grazed to 1000 lbs/ac residual vegetative dry matter (RDM), and iii) grazed to 500 lbs/ac RDM. Grazing did not increase sediment, nutrient or pathogen concentrations in streamwater until residual dry matter levels were decreased to less than 1000 lbs/ac. Microbial pathogen parameters, such as fecal coliforms, can be elevated above water quality standards even in the complete absence of grazing, suggesting that wildlife provide an appreciable background level of some microbial pathogens. We found about 95% of all samples have Cryptosporidium parvum levels below our detection limit (5 oocysts/L) and only trace numbers (<10 oocysts/L) in positive samples. Further, our results indicate that fecal coliform concentrations are not a suitable indicator for C. parvum on grazed annual rangeland watersheds. However, turbidity might serve as an adequate, low cost indicator for E. coli and fecal coliforms. This study demonstrates that proper grazing practices result in minimal impact on nutrient, sediment and microbial pathogen export from the studied watersheds.

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[2] Rangeland Watershed Specialist, University of California, Davis Department of Plant Sciences One Shields Avenue 1210 Plant and Environmental Sciences Bldg Davis, CA 95616-8780. e-mail: kwtate@ucdavis.edu.

[3] Professor, Pedologist, Soil Mineralogist-AES, University of California, Davis Soils & Biogeochemistry Program 3134 Plant and Environmental Sciences Building Davis, CA 95616. e-mail: radahlgren@ucdavis.edu.

[4] Associate Specialist, University of California Cooperative Extension, Tulare County. e-mail: ratwill@vmtrc.ucdavis.edu.

[5] Watershed Management Advisor, University of California Cooperative Extension, Sonoma County, 133 Aviation Boulevard, Suite 109 Santa Rosa, CA 95493. e-mail: djllewis@ucdavis.edu.

[6] Mendocino County Director and Livestock & Natural Resources Advisor, University of California Cooperative Extension, Mendocino County 890 N. Bush Street Ukiah, CA 95482. e-mail: jmharper@ucdavis.edu.

[7] Assistant Vice President - Programs, Statewide Leader for Cooperative Extension, Director of the Research and Extension Centers, and Professor and Russell Rustici Chair in Rangeland Management, University of California Agriculture and Natural Resources 1111 Franklin St. Franklin 6401 Oakland, CA 94607-5200. e-mail: barbara.allen-diaz@ucop.edu.

Prioritizing Oak Woodland Conservation Through a Countywide Strategic Acquisition Plan[1]

Tom Robinson,[2] Emily Heaton,[3] Misti Arias,[4] and Kathleen Brennan Hunter[5]

Abstract

In 1990, residents of Sonoma County approved two measures, one to create the Sonoma County Agricultural Preservation and Open Space District, and a second to levy a 1/4 percent sales tax for 20 years in order to provide funding. The District's mission calls for the protection of Sonoma County's "community separators, scenic corridors, critical habitat areas, and biologically significant areas affected by development," all of which intersect with oak woodland. To implement the voters' mandate, the District periodically prepares a strategic acquisition plan to identify priority conservation areas. We present here a process of mapping core oak woodlands and demonstrate how the District uses these data to prioritize oak woodlands in Sonoma County for conservation. First, we used Geographic Information System (GIS) technology to map large patches of continuous tree cover that are at least 50m from land that is developed or in intensive agriculture. These core forest-woodland patches are assumed to provide relatively high quality habitat for wildlife, as well as important ecosystem services. Oak-dominated communities within core forest-woodland were then identified using a detailed vegetation map for Sonoma County. Finally, results from land-use change models provided information about core oak woodland that is threatened by residential and vineyard development. The District will use this information, as well as data layers that show land that is currently protected and other priorities for the District (e.g. priority viewsheds), to identify areas where protection of oak woodlands is most critical.

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[2] Conservation GIS Analyst, Sonoma Co. Agricultural Preservation & Open Space District 747 Mendocino Ave., Ste. 100 Santa Rosa, CA 9540. e-mail: trobins1@sonoma-county.org.

[3] UC Berkeley Department of Environmental Science, Policy, and Management. e-mail: eheaton@nature.berkeley.edu.

[4] Interim Conservation Program Manager, Sonoma Co. Agricultural Preservation & Open Space District. e-mail: marias@sonoma-county.org, kbrennan@sonoma-county.org.

Stoiochiometry of Carbon and Nitrogen Transfer in Blue Oak Seedlings[1]

Laura M. Suz,[2] Victoria Albarracin,[3] and Caroline S. Bledsoe[4]

Abstract

In California's oak woodlands, survival and growth of the dominant oak species depends on the symbiotic relationship between oaks and certain fungi that form ectomycorrhizae on oak roots. Ectomycorrhizal fungi (ECMF) are major players in carbon (C) and nitrogen (N) utilization and cycling, facilitating water and nutrient uptake from the soil into the plant, while the plant supplies carbon to their fungal partners. Little is known about whether nitrogen uptake is directly related to a high acquisition of carbon from the host. Our study explored this potential linkage between carbon and nitrogen flows in plant-ECMF interactions. We hypothesized that nitrogen and carbon fluxes are linked, so that mycorrhizal roots with more 15N will be stronger sinks for 13C from their oak hosts. We used the stable isotopes 13C and 15N to trace the fluxes of these two elements in oak seedlings, particularly in their fine ECM-roots. In a greenhouse study, we added 15NH4Cl to the soil in a pot containing blue oak (Quercus douglasii Hook and Arn.) seedlings. After 2 weeks, we added 13C glucose or 13C sodium bicarbonate to oak foliage. We sampled fine roots 1 and 4 days after the 13C source was added. After 12 days we harvested the entire seedling. We separated the plant into leaves, branches, stem and roots: tap-root, medium roots, fine and mycorrhizal roots. We analyzed the plant tissues for 15N and 13C. Preliminary results show that after 4 days 13C from glucose began to be detected in roots. Carbon as sodium bicarbonate was not detected in mycorrhizal roots even after 12 days. Nitrogen as 15N was detected in roots 15 days after and in leaves 27 days after soil application. The stoiochiometry of nitrogen and carbon in the roots can help explain the mycorrhizal sink strength for both elements in oak seedlings.

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[2] PhD student. Centre Tecnològic Forestal de Catalunya, Solsona, Spain ES-25280. e-mail: laura.martinez@ctfc.es.

[3] PhD student and professor, respectively, Department of Land, Air, and Water Resources, University of California, Davis, CA 95616. e-mail: mvalbarracin@ucdavis.edu.

[4] PhD student and professor, respectively, Department of Land, Air, and Water Resources, University of California, Davis, CA 95616. e-mail: csbledsoe@ucdavis.edu.

Combined Development and Climate Change Impacts on Blue Oak Woodlands[1]

Nathaniel Snider,[2] Zachary Bradford,[3] Ryan Digiondomenico,[3] Sarah Graber,[3] Stephanie Hsia,[3] Lee Hannah,[4] and Chang Wan Seo[5]

Abstract

Development and climate change present threats to blue oaks (sp. *Quercus douglasii*) at short time scales and large spatial scales relative to the species life history and dispersal ability. We model several development and climate change scenarios for the Southern Sierra Foothills and determine the patterns of blue oak habitat reduction expected from each threat. We measure the percent of present-day habitat lost for three different time horizons and make recommendations for management of this ecologically and economically beneficial species. The human population in the counties of the Southern Sierra Foothills is expected to double in the next ten years, creating intense pressure for development. Depending on where development takes place, the resulting modifications to the landscape will impact blue oak woodlands to varying degrees. We examine different development scenarios reflecting realistic policy alternatives and evaluate the expected loss of blue oak woodlands under each case. Over the past 150 years, the ecology of blue oak woodlands has been dramatically modified, and climate change will produce even further ecological modifications. Blue oak regeneration is constrained by climatic conditions and other factors, which combine to produce the spatial distribution of blue oak woodlands. We use regional climate models in conjunction with soil types and observed species distributions to model the bioclimatic envelope of the blue oak. We then determine the expected shift in blue oak spatial distributions under a range of climate change scenarios. In order to ensure the continued vitality of blue oak woodlands in this region, planners will need to consider both the near-term pressures of development and the longer-term impacts of climate change. We evaluate the impacts of each threat for three different time horizons: 2010, 2025, and 2050. The combination of these threats may require a long-term plan that takes the dynamics of both threats into account.

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[2] Donald Bren School of Environmental Science & Management, University of California, Santa Barbara 2400 Bren Hall Santa Barbara, CA 93106-5131. e-mail: nsnider@bren.ucsb.edu.

[3] Donald Bren School of Environmental Science & Management, University of California, Santa Barbara. e-mail: zbradford@bren.ucsb.edu, rdigiondomenico@bren.ucsb.edu, sgraber@bren.ucsb.edu, shsia@bren.ucsb.edu.

[4] Research Fellow Biodiversity Corridor Design, Conservation International Center for Applied Biodiversity Science 2011 Crystal Drive, Suite 500 Arlington, VA 22202.

[5] Seoul National University.

Lessons Under the Oak Tree: A Writer's Perspective[1]

Karen Kluger[2]

Abstract

While walking among the oak groves near my home in Thousand Oaks, CA, I found much wisdom hidden in nature. The wisdom has always been there for humankind to find. About this same time, I learned Native Americans call people and trees the earth's only "Standing Ones." Respecting Native American's insights, I grew more observant of the connections people have to trees. I began to surmise that creation may consist of a limited number of building blocks ingeniously re-arranged, much like only ten numbers are re-arranged to create all the world's telephone numbers. For example, trees and people begin life either planned or unplanned. In the first category there are Christmas tree farms and orchards that are planned as surely as a couple that conceives with fertility drugs or in vetro. Yet, for all the planning humans do, most life starts as a wild thing. At night in bed a couple snuggles under the covers, things heat up. Only one sperm out of thousands needs to join a woman's egg for a new life to begin. Outdoors, a similar happening occurs, but more slowly. The male-like erect tree also releases thousands of seeds, yet few will sprout, which gives new meaning to the Biblical saying, "many are called, but few are chosen." After seeds litter the ground, autumn leaves fall forming a blanket on earth's bed. Then the rains come, as in foreplay, moistening the dry leaves. Under a blanket of composting leaves, heat is generated, encouraging germanation. The beginning of life is humble, silent. The seed sends out a root hair that connects it to mother earth, the same way the placenta connected each of us to our mother. When it's time for birth, the seed casing dilates, enabling a tender leaf to emerge, just as at birth, an infant with soft bones emerges through a dilated canal. When we stop to admire a lovely tree, on subconscious level, we are connecting to our own humble beginning and to nature's splendor that resides within ourselves. The insights in the grove became the book, "Lessons Under the Oak Tree." Topics include nature's balance and the danger of imbalance; the value of imperfections; the deeper meaning of sudden oak death; evolution, another name for freedom of choice; the wisdom for us in how trees heal after a serious loss, and forests of the future. Finally, the book is the story of how I learned that life can be as simple as a tree and not as complicated as the forest.

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[1] This paper summarizes a poster that was presented at the Sixth California Oak Symposium: Today's Challenges, Tomorrow's Opportunities, October 9-12, 2006, Rohnert Park, California

[2] For more information, see: www.karenkluger.com. e-mail: karenkluger@earthlink.net.

Oak Decline, Experimental Weather Modification and Climate Change[1]

Rosalind Peterson[2]

Abstract

Many trees in Mendocino, Lake and Sonoma Counties (California), are in declining health. An entire suite of plant communities, including wide varieties of trees, are in decline. NOAA reports over 80 ongoing experimental weather modification programs in the Western States in 2005, that may have changed weather patterns in California and adversely impacted our trees. And now U.S. Senate Bill 517, a bill that would allow experimental weather modification by artificial methods and implement a national weather modification policy is soon to be passed. This bill does not include agriculture, natural resources, or public oversight. The appointed Board of Directors established by this bill does not include any agricultural, water, EPA, or public representatives, and has no provisions for Congressional, State, County, or public oversight of their actions or expenditures. In addition, NASA also notes (October 2005 Newsletter), that increasingly persistent contrails are "...trapping warmth in the atmosphere and exacerbating global warming..." NASA also goes on to say that "...Any increase in global cloud cover will contribute to long-term changes in the Earth's climate. Likewise, any change in Earth's climate may have effects on natural resources..." The overall impact of persistent jet contrails and man-made clouds changing our weather should be considered in any tree health studies. The 1999, EPA, SUBSONIC JET EMISSIONS REPORT, ENVIRONMENTAL PROTECTION AGENCY PA420-R-99-013 - Final Report "Evaluation of Air Pollutant Emissions from Subsonic Commercial Jet Aircraft", U.S. Environmental Protection Agency April 1999, details in depth crop and vegetation damage from these emissions. Are we taking into consideration the impact of jet fuel emissions when considering tree health decline? Weather Modification may adversely impact watersheds, trees, agricultural crops and water supplies. And who is going to decide the type of weather modification experimentation in the future and who it will benefit or adversely impact? When you add atmospheric heating (H.A.A.R.P.) and testing (NOAA CRRES / Barium & TMA / trimethyl aluminum), to over 80 weather modification programs, the mix will have a tremendous impact on tree and plant communities and micro-climates. It is important that we understand the complex nature of the items listed above and determine how they will impact the natural environment in which we live. We are dependent on our trees, agricultural crops, and water supplies. If they are being adversely impacted then we need to do the studies to see what impacts these changes are having on our environment. Our survival depends on our understanding the overall forces at work and being able to influence legislation to benefit all of us and ultimately to protect our food supplies, water, and the health of our trees.

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[1] This paper summarizes a poster that was presented at the Sixth California Oak Symposium: Today’s Challenges, Tomorrow’s Opportunities, October 9-12, 2006, Rohnert Park, California.

[2] Former CA USDA Agriculture Crop Loss Adjustor, PO Box 499 Redwood Valley, CA 95470. e-mail: info@californiaskywatch.com.

Bird Monitoring of an Oak Woodland Stream[1]

Gregory A. Giusti,[2] Robert Keiffer,[3] and Charles Vaughn[3]

Abstract

The results of nearly 15 years of avian monitoring will be presented. The data describes the occurrence of nearly 100 species, representing 20 families and 9 orders.

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[1] This paper summarizes a poster that was presented at the Sixth California Oak Symposium: Today's Challenges, Tomorrow's Opportunities, October 9-12, 2006, Rohnert Park, California.

[2] North Coast Area Hardwoods Advisor, Mendocino County UCCE, 890 N. Bush Street, UCCE-Mendocino County, Ukiah, CA 95482.

[3] University of California HREC. E-mail: rjkeiffer@ucdavis.edu; , mcevaughn@ucdavis.edu.

Fuel Dynamics in Oak Woodlands: Effects of Sudden Oak Death[1]

Travis Freed,[2] Scott Stephens,[3] and Maggi Kelly[4]

Abstract

The rapid accumulation of fuel due to SOD is a result of the death and structural failure of oak trees. In addition, canopy removal will likely change microclimatic variables such as wind speed and incident radiation. These changes will result in a shifting of understory composition in the longer term, likely favoring invasive species that increase fire return interval and fire intensity. In the short term, the increase in incident solar radiation will lower relative humidity and hasten the drying of fuels. These factors would increase the probability of a high intensity wildfire. Increased fire intensity and flame lengths will increase the likelihood of crown fire initiation. Larger more intense fires could cause changes that reduce the ability of an ecosystem to recover. A better understanding of what is causing fuel accumulation can help to improve the accuracy of fire modeling and help guide management decisions. The focus of this study is to understand the ecological factors associated with fuel accumulation in coastal oak woodlands. This study hypothesizes that sudden oak death (SOD) is the most significant factor in recent fuel accumulation in Marin County's coastal oak woodlands. To test this hypothesis, ecological and stand structure variables were measured to determine which variables most strongly predict fuel changes. Fuel measurements in 2002 and 2004 showed an increase in fuel levels. Plots were separated into those with a strong oak component and those with very little or no oak. The Oak group was then further divided between plots that showed signs of bleeding in 2001 and those with no signs of bleeding. The highest fuel levels were measured in forests that had oak trees with some bleeding in 2001.

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[2] M.S. Environmental Science, Policy and Management University of California Berkeley. e-mail: tfreed@nature.berkeley.edu.

[3] Associate Professor of Fire Sciences University of California Berkeley. e-mail: stephens@nature.berkeley.edu.

[4] University of California Berkeley. e-mail: mkelly@nature.berkeley.edu.

Landscape-Scale Relationships Between Oak Recruitment and Livestock Management[1]

W. Stanley Harpole,[2] Katharine Suding,[2] Mitchel McClaran,[3] and Rebecca Aicher[4]

Abstract

There is concern that natural oak recruitment in California is not sufficient to maintain current populations. In particular, the inability of oak seedlings to transition to sapling and adult stages may often constrain recruitment. Grazing by cattle is often implicated as having potentially positive or negative effects on recruitment that may be dependent on the season of grazing. Grazing, in general, by removing litter, might promote seedling establishment. But grazing could also decrease survival and transitions to sapling and tree stages depending on whether grazing occurs during the dormant season or the growing season. Thus, we hypothesize that appropriately timed grazing may play a positive role in the recruitment of oaks in this system. Here we present results from a landscape-scale survey of blue oak (*Quercus douglasii*) seedlings and saplings at the Sierra Foothills Research and Extension Center. We found similar sapling density in dormant season grazed, growing season grazed, and ungrazed pastures. Seedling density, however, was greater in grazed pastures than in ungrazed pastures. We also present preliminary results exploring seedling survival in relationship to grazing season and plant community composition.

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[2] University of California, Irvine. E-mail: wharpole@uci.edu, ksuding@uci.edu.

[3] Professor of Range Management, University of Arizona School of Renewable Natural Resources Biological Sciences East 325 Tucson, AZ 85721. e-mail: aran@u.arizona.edu.

[4] University of California, Irvine. e-mail: raicher@uci.edu.

State and Transition Models for California's North Coast Oak Woodlands[1]

John Harper,[2] Stephanie Larson,[3] Morgan Doran,[4] Michael Lennox,[5] Maximo Alonso,[6] Craig Thomsen,[7] and Melvin George[8]

Abstract

University of California Cooperative Extension and USDA Natural Resources Conservation Service are developing ecological site descriptions for the oak woodlands in Major Land Resource Area 15 which includes California's north and central coasts. Vegetation surveys conducted during the spring and summer of 2004 and 2005 determined woody plant canopy cover and density, and understory cover, production and species composition. On the north coast initial site delineation is based on understory productivity, density and canopy cover of the dominant blue oak (*Quercus douglasii*) and its associates coast live oak (*Q. agrifolia*), black oak (*Q. kelloggii*), valley oak (*Q. lobata*), manzanita (*Arctostaphylos* spp), and poison oak (*Toxicodendron diversiloba*). Blue oak savanna or woodland with a grass understory and few shrubs or understory trees is common and often intermixed with other oak woodland communities or shrub communities. While succession has not been extensively studied in oak-woodland ecosystems, state and transition models are being developed for the long-lived tree and shrub layers based on their response to fire, grazing and vegetation management. Shorter term dynamics of the annual plant dominated understory are also included in the state and transition models.

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[1] This paper summarizes a poster that was presented at the Sixth California Oak Symposium: Today's Challenges, Tomorrow's Opportunities, October 9-12, 2006, Rohnert Park, California.

[2] Mendocino County Director and Livestock & Natural Resources Advisor, University of California Cooperative Extension, Mendocino County 890 N. Bush Street Ukiah, CA 95482. e-mail: jmharper@ucdavis.edu.

[3] Livestock, Range Management Advisor, University of California Cooperative Extension Sonoma County, Sonoma County 133 Aviation Boulevard Suite 109 Santa Rosa, CA 95403-2894. e-mail:: slarson@ucdavis.edu.

[4] Advisor for Livestock and Natural Resources University of California Cooperative Extension Solano County 501 Texas Street, First Floor Fairfield, CA 94533-4498. e-mail: mpdoran@ucdavis.edu.

[5] Staff Research Assistant, University of California Cooperative Extension, Sonoma County 133 Aviation Boulevard Suite 109 Santa Rosa, CA 95403-2894. e-mail: mlennox@ucdavis.edu.

[6] Graduate Student, University of California, Davis, Department of Plant Sciences One Shields Avenue 1210 Plant and Environmental Sciences Bldg Davis, CA 95616-8780. e-mail: malonso@ucdavis.edu.

[7] Research Associate, University of California, Davis. e-mail: cdthomsen@ucdavis.edu.

[8] Specialist, University of California, Davis, Dept. of Plant Sciences One Shields Avenue 1210 Plant and Environmental Sciences Bldg Davis, CA 95616-8780. e-mail: mrgeorge@ucdavis.edu.

State and Transition Models for California's Central Coast Oak Woodlands[1]

Royce Larsen,[2] Sheila Barry,[3] Theresa Ward,[4] Karl Striby,[5] Ken Oster,[6] Craig Schriefer,[7] and Maximo Alonso[8]

Abstract

University of California Cooperative Extension and USDA Natural Resources Conservation Service are developing ecological site descriptions for the oakwoodlands in Major Land Resource Area 15 which includes California's north and central coasts. Vegetation surveys conducted during the spring and summer of 2004 and 2005 determined woody plant canopy cover and density, and understory cover, production and species composition. Data from these surveys and soil characteristics from SSURGO are being used to delineate and name ecological sites. Ecological site descriptions include state and transition models that describe the dynamics of the dominant species. Central coast blue oak (*Quercus douglasii*) woodlands and coast live oak (*Q. agrifolia*) woodlands are often associated in a mosaic with coastal sage scrub, chaparral and annual grassland communities. Some researchers have correlated these mosaics with geological substrates and soil characteristics. However, other researchers have found each of these vegetation types on most geological and soil types suggesting that disturbance and biological factors, such as fire, grazing and competition, are important determinants of these mosaics. Fire and grazing are the primary disturbances in these vegetation types. Consequently fire frequency, recovery from fire and grazing are important themes in the state and transition model for the central coast vegetation mosaic.

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[1] This paper summarizes a poster that was presented at the Sixth California Oak Symposium: Today's Challenges, Tomorrow's Opportunities, October 9-12, 2006, Rohnert Park, California.

[2] Area Natural Resources Advisor, University of California Cooperative Extension 2156 Sierra Way Suite C San Luis Obispo, CA 93401. e-mail: relarsen@ucdavis.edu.

[3] Livestock & Natural Resources Advisor, University of California Santa Clara County 1553 Berger Drive, Bldg. 1 San Jose, CA 95112. e-mail: sbarry@ucdavis.edu.

[4] University of California Cooperative Extension. e-mail: taward@ucdavis.edu.

[5] Rangeland Management Specialist, USDA NRCS 65 Main Street, Suite 108 Templeton, CA 93465. e-mail: karl.striby@ca.usda.gov

[6] Area Soil Scientist, CA NRCS 318 Cayuga Street, Suite 206 Salinas, CA 93901-2668.

[7] Lab Assistant, University of California, Davis, Department of Plant Sciences One Shields Avenue 1210 Plant and Environmental Sciences Bldg Davis, CA 95616-8780. e-mail: cschriefer@ucdavis.edu.

[8] Graduate Student, University of California, Davis, Department of Plant Sciences One Shields Avenue 1210 Plant and Environmental Sciences Bldg Davis, CA 95616-8780. e-mail: malonso@ucdavis.edu.

Historical Distribution of Oak Species in the Central and Northern Sierra Nevada[1]

Sarah Thrasher,[2] Jaquelyn Bjorkman,[2] Boynton Ryan,[2] and Rodd Kelsey[2]

Abstract

This poster presents the historical distribution of six tree and four shrub species in the genus *Quercus* for the central and northern Sierra Nevada Mountains. The species maps are derived from the Wieslander Vegetation Type Mapping (VTM) Project, which produced vegetation maps and vegetation plot data for California in the 1930s. Methods to render the archival versions of these maps to GIS-compatible digital versions were developed, and an area covering 49,500 km2, was developed. The GIS version of the maps were then queried for each oak species and summary information recorded. We present maps for each species, a summary of their spatial extents, elevation distribution, and a summary of the size class and structure of each species, as derived from the VTM plot data. The electronic versions of the individual species range maps will permit assessment of loss of oak habitats when compared with modern vegetation maps.

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[1] This paper summarizes a poster that was presented at the Sixth California Oak Symposium: Today's Challenges, Tomorrow's Opportunities, October 9-12, 2006, Rohnert Park, California.

[2] Junior Specialist-GIS, Dept. of Environmental Science and Policy University of California, Davis 2132 Wickson Hall, 1 Shields Ave. Davis, CA 95616. e-mail: slthrasher@ucdavis.edu, jhonig@ucdavis.edu, rboynton@ucdavis.edu, trkelsey@ucdavis.edu.

Occupancy Estimation Models of Focal Bird Species in Sierra Nevada Foothill Woodlands[1]

Eric Wood,[2] Matt Johnson,[2] and Barrett Garrison[3]

Abstract

The California Native Plant Society Vegetation Monitoring Program (CNPS VMP) may provide habitat data useful for wildlife research. In 2004-2005, point counts for bird occurrences and Rapid Assessment (RAP) and Relevé vegetation surveys following CNPS VMP protocols were completed in the Sierra Nevada Foothill Blue Oak (*Quercus douglasii*) Woodlands of Yuba County, California. Occupancy estimation models were built for Acorn Woodpecker (*Melanerpes formicivorus*), White-breasted Nuthatch (*Sitta carolinensis*) and Ash-throated Flycatcher (*Myiarchus cinerascens*). Testing data were collected in 2006 and compared to the training models for validation. Estimates of occupancy were accurate at 90% of randomly selected re-sampled points for Acorn Woodpecker, 80% for White-breasted nuthatch and 85% for Ash-throated flycatcher. The results show both the Relevé and RAP protocols of the CNPS VMP include important habitat data useful for species-specific predictive bird modeling within Sierra Nevada Foothill Hardwood Rangelands. Further work should focus on continued validation of CNPS VMP models for different species in varying plant communities.

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[2] Humboldt State University 4044 Lanphere Rd. Suite A Arcata, CA 95521. e-mail: emw34@humboldt.edu, mdj6@humboldt.edu.

[3] Staff Environmental Scientist, Sacramento Valley-Central Sierra Region, California Department of Fish and Game, 1701 Nimbus Road, Rancho Cordova, CA 95670 (printed posthumously).

UC Master Naturalist Program[1]

Julie Fetherston,[2] Adina Merenlender,[3] and Greg Giusti[4]

Abstract

Sustaining our natural resources requires increased understanding of science, adaptive management, and cooperation among diverse interest groups. In California as population increases, patterns of development and demographics are changing and we need an active and well informed public to participate in resource conservation. In an effort to provide meaningful service learning opportunities for this public and support to professional naturalists, scientists and educators we are developing a UC Master Naturalist program. This comprehensive statewide natural resources education program is modeled on the highly successful UC Master Gardener program and will provide adult volunteers with science-based training in ecology, natural and cultural history and interpretive techniques. The 40+ hour training course will be designed to produce a core of knowledgeable volunteers ready to participate in restoration projects, monitoring, research, educational outreach and community activities designed to enhance natural resource conservation. To begin we are establishing partnerships and support, developing curriculum, and implementing pilot chapters. Ultimately a self sustaining statewide program will benefit resource agencies, educational institutions, land managers and communities.

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[2] e-mail: julief@pacific.net.

3 Specialist, Department of Environmental Science, Policy, and Management, 137 Mulford Hall, University of California, Berkeley, CA 94720.

[4] North Coast Area Hardwoods Advisor, Mendocino County UCCE, 890 N. Bush Street, UCCE-Mendocino County, Ukiah, CA 95482..

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