

Chapter 15. Grazing ecology of California grasslands

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Introduction

Grazing is an ecosystem process broadly defined as feeding on herbaceous plants, algae, fungi, or phytoplankton (Begon et al. 1996). Here we constrain our review to the effects of grazing by large mammals on herbaceous plants and selected animals in California's grasslands, savannas, and associated herbaceous riparian areas. A brief history of grazing in California grasslands is provided to illustrate that while livestock grazing is a relatively recent phenomenon, California grasslands have always been grazed by large and small animals, albeit in many different ways.

We describe the grazing process as comprised of three phenomena: defoliation, trampling, and nutrient redistribution. However, research explicitly linking these processes to plant responses at the individual, population, and community levels of ecological organization are lacking for California grasslands. Hence, we rely largely on phenomenological research generated by range scientists studying productivity and composition responses to grazing management. This work has shown that California annual grassland productivity can be effectively managed for livestock production via manipulation of grazing intensity (Bartolome et al. 1980), but that species composition is more or less entrained by intra- and inter-annual weather (Jackson and Bartolome 2002). Because of this, these annual grasslands have been characterized as nonequilibrium systems, where plant-plant and plant-animal interactions are of

minimal importance relative to abiotic constraints (Wiens 1984). Alternatively, equilibrium systems are those where biotic interactions such as competition and herbivory are key drivers of plant community structure. Some evidence exists that perennial dominated herbaceous communities in California behave in a more or less equilibrium manner (Jackson and Allen-Diaz 2006).

We then expand our discussion to grazing effects on native and non-native, invasive plant species and the grassy understory of savanna trees. California grasslands are components of a broader landscape mosaic that includes tree canopies and riparian corridors. Therefore, we discuss grazing effects on oak savanna understory vegetation, which is usually dominated by annual grasses and forbs. We discuss grazing impacts here but only where the presence of the canopy is known to modify disturbance dynamics observed in open grasslands or where no information exists for open grasslands. Similarly, grazing effects on the herbaceous component of wetlands and riparian areas are discussed, while grazing impacts on shrubs and woody vegetation are not. Finally, we briefly discuss grazing effects on California grassland wildlife and note ways in which grazing by non-domestic large mammals such as elk differs from grazing by livestock.

Brief history of grazing in California grasslands

Grasses appear in the North American fossil record during the Eocene (45 to 55 million years ago) somewhat coincident with the advent of high-crowned teeth in mammals (Janis et al. 2002, Stromberg 2002). Grasses have evolved habits (prostrate growth) and structures (basal meristems, awned spikelets, and silica deposits in cell walls) to avoid or tolerate aboveground tissue loss (Briske 1991), and typically respond to defoliation with elevated relative growth rates

(Ferraro and Oesterheld 2002). Hence, the removal of plant tissue (e.g. disturbance) is a fundamental process in the grassland biome (Knapp et al. 1999, Woodward et al. 2004, Bond et al. 2005).

The earliest California grass fossils date to the Pliocene (5.4 to 2.4 million years ago) (Axelrod 1944), so grazing animals have been more or less a part of California grassland, savanna, and woodland ecosystems for millenia (Edwards 1992). Before Eurasian contact in 1769 and the establishment of widespread cattle, sheep, and horse grazing, as well as market hunting (Burcham 1957, Burcham 1975), large herds of pronghorn antelope and tule elk grazed California grasslands (Edwards 1996). Prehistoric descriptions of California grassland vegetation are chronicled in Bartolome et al. (In press), Edwards (1992) and other chapters in this volume (Chapters 4, 5). These accounts all paint a picture of dynamic systems where grazing, along with other disturbances such as fire (Chapters 5 and 18), are fundamental evolutionary and ecological processes.

The composition of herbaceous vegetation in California prior to Eurasian contact is unknown. Many believe native perennial grasses, particularly the bunchgrass *Nassella pulchra*, once were much more abundant (Clements 1934, Beetle 1947, White 1967, Heady 1977). Hamilton (1998) has rather convincingly argued against overuse of this paradigm, citing over-extrapolation of Clements's climax community concept (Clements 1936) and the dogma that has derived from it. He suggested that native annuals or shrubs were once dominant, especially in drier parts of the grassland. Holstein (2001) argued that the rhizomatous perennial grass, *Leymus triticoides*, dominated the pre-agricultural Central Valley floor. However, his analysis partially relied on the relict method for which he and others criticize Clements. The relevance of this discussion to grazing ecology of California grasslands is that dramatic increases in livestock

grazing intensity in the late 19th Century are often implicated as one of the main drivers of the shift from a perennial grassland flora to one dominated by annuals (Burcham 1975).

Burcham (1957) reviewed the history of human colonization of California and concomitant livestock introductions. The use of the California grasslands for domestic livestock production began with Spanish colonization in 1769 and establishment of missions along the coast, but significant livestock grazing began around 1773 (Bartolome et al. In press).

Widespread grazing expanded inland beginning in 1824 when land was granted for vast cattle ranchos. Livestock data for the 19th and early 20th centuries showed that cattle and sheep densities were highly variable from county-to-county and year -to -year, but averaged around about 4 million head (Ewing et al. 1988). Since 1970, cattle numbers have remained constant fairly consistent at about 5 million head (USDA-NASS 2006). Sheep densities began a steep decline in 1960 when their numbers went from about 2.5 million head, which had been their 100-y average, to less than 0.5 million head by 2004 (USDA-NASS 2006).

Present day classification of California grasslands fall along geographical boundaries with two main sub-types, perennial grass-dominated *Coastal Prairie* and annual grass-dominated *Valley Grassland* (Bartolome et al. In press). Recently, a third sub-type, *Coast Range Grassland*, was shown to be floristically distinct, exhibiting a relatively even distribution of perennial and annual grasses (Jackson and Bartolome 2002). However, little specific information is available for this association so we rely largely on information generated from the two broad grasslands categories both of which grade into areas of increasing oak (*Quercus* spp.) cover (Allen-Diaz et al. 1997).

The grazing process and its management

Grazing affects grasslands directly by removing leaf area via defoliation, compacting soils via trampling, and altering biogeochemical cycles by redistributing nutrients in time and space (Heitschmidt and Stuth 1991, Heady and Child 1994). Impacts from each of these phenomena can be manifested at various scales including the genetic, individual, population, community, and/or ecosystem levels of ecological organization. Furthermore, the relative importance of these factors may be dependent on site and time-specific variables that are naturally dynamic, for instance, an understanding of grazing effects for tallgrass prairie is not likely transferrable to annual grassland. In fact, grassland responses to grazing between two climatically distinct regions of California grassland may be more different than responses between California coastal prairie and Midwestern tallgrass prairie, which are both dominated by perennial grasses. Hence, making generalizations about grazing responses across California grasslands is tenuous at best (Bartolome 1989).

When considering the effects of large herbivores on grasslands it is useful to classify by the type of animal, as well as the intensity, timing, frequency, and duration of grazing (Heady and Child 1994). Common grazing animals in present day California grasslands are cattle and sheep (livestock), as well as elk, deer, gophers, voles, moles, grasshoppers, and other arthropods. The grazing intensity of a particular animal is defined as the proportion of forage (phytomass available for grazing or browsing) removed. It may be measured in a variety of ways, but for grasses it is usually determined by estimating the amount of phytomass before and after a grazing period. Because grazing intensity is strongly linked to defoliation responses by the plant and its ability to compensate for loss of herbage, this parameter is a very important aspect of grazing management (Bartolome 1993). The timing, frequency, and duration of grazing also are

important in determining the impacts of grazing on target plant species (Heady and Child 1994). These factors often interact with animal preference and plant palatability and thus can be keys to developing grazing prescriptions and understanding the effects of different kinds of grazers (Sampson 1952). Nonetheless, overall there are few quantitative studies comparing the effects of different types of grazers in California grasslands.

Defoliation

The most direct effect of an herbivore on a plant is to selectively reduce leaf area, which results in a short-term loss of carbon gain (Del-Val and Crawley 2005). How the plant responds to reduced photosynthetic capacity largely dictates how the individual will fare. Hence, defoliation intensity, environmental stress, grazing history, genetic potential, and biotic constraints such as competition and life history stage interact to determine the plant's fate. Lemaire and Chapman (1996) cite two general responses to defoliation: 1) short-term redistribution of carbon and nitrogen within the plant and 2) long-term morphogenetic response where the shape of the plants in a community change over time. Upon defoliation, grasses draw on carbohydrate and nutrient reserves stored in non-photosynthetic structures, such as root crowns, roots, and rhizomes, but the magnitude of this reallocation of internal plant resources is related to the remaining leaf area. If some photosynthetic tissue remains after defoliation, regrowth is primarily from carbon gain via photosynthesis (Richards and Caldwell 1985). However, root:shoot ratios of perennial grasses decline as a result of defoliation (Ferraro and Oosterheld 2002) because carbon gained from photosynthesis is mainly allocated aboveground to rebuild photosynthetic apparatus (Turner et al. 1993). Such changes in allocation and re-allocation are thought to translate to population-level effects in perennial grasslands because these responses are species-specific (Dyer et al. 1993, Damhoureyeh and Hartnett 2002).

Whole-plant responses of several species of annual grasses to variation in the frequency and timing of defoliation were evaluated in a series of pot experiments in the early 1960s (Savelle and Heady 1970). Generally, these studies showed that shorter stature species like *Bromus madritensis* and *Vulpia bromoides* were able to grow more rapidly and reproduce better under higher frequency and later-season clipping in pots than were taller species like *Bromus diandrus* and *Avena barbata*. Validation of these pot studies *in situ* has not occurred. In annual grasslands, population-level responses to grazing intensity gradients are hypothesized to arise from soil seedbank alteration from multiple years of grazing pressure (Pitt and Heady 1979, Rosiere 1987, Heady et al. 1992), but these effects are difficult to separate given the overriding influence of intra- and inter-annual weather fluctuations on the plant community (Bartolome 1979).

Morphogenetic responses are common in perennial grasslands elsewhere (Holland et al. 1992), but have not been documented in California grasslands. Shorter stature annual plants benefit from defoliation events relative to taller stature annual grasses (Savelle and Heady 1970) and therefore their progeny should preferentially propagate. This should allow them to persist within grasslands where taller stature species would otherwise be competitive dominants.

Holland et al. (1992) showed that perennial grasses from an area with a history of grazing produced greater biomass after experimental defoliation than conspecifics from areas without a grazing history in Colorado shortgrass steppe. These short- and long-term responses are thought to contribute to compensatory growth—the ability of a plant to regrow at faster rates post-defoliation such that total biomass at season's end is equal to an undefoliated conspecific (McNaughton 1979). This phenomenon has been reported for several systems (Williamson et al. 1989, Hik and Jefferies 1990), but Ferraro and Oesterheld's (2002) meta-analysis showed it was

not a general response in individual plants. Field studies where plants are growing in competition with each other further cloud the issue. Leriche (2003) modeled compensatory growth showing that resource availability modulated the sign of response, i.e. whether plants under- or over-compensated for defoliation depended on the resource status of the system. These phenomena have not been demonstrated in annual grasslands or for native perennial grasses in California.

Determining the effects of defoliation on the structure and productivity of the plant community depends on the spatial and temporal scale examined (Bartolome 1989). In one study of sheep in annual grassland, the selective nature of grazing was confirmed, but was not subsequently manifested in changes in plant abundance (Bartolome and McClaran 1992). The inability to reliably scale up research to the community and landscape levels of organization has severely compromised prediction of defoliation and grazing effects in California grasslands (Bartolome 1993, Hayes and Holl 2003b).

Trampling

Ungulates physically alter soil structure because their rather substantial mass, as much as 1000 kg per animal, is carried by relatively small hooves. The usual effect is compaction, which is quantified as bulk density (Pietola et al. 2005), however, compaction responses can be negligible. Increases in soil compaction result in reduced infiltration rates, which in turn increase surface runoff and erosion (Daniel et al. 2002). Trampling effects in California grasslands are not uniform because livestock preferentially use areas near shade and water sources (Tate et al. 2003). That said, two independent studies found that light to moderate livestock grazing in and around riparian areas of oak savanna did not significantly alter the morphology of streambanks (Allen-Diaz et al. 1998, George et al. 2002). However, it has been

observed frequently that heavy grazing can reduce vegetation cover and decrease the slope of streambanks resulting in bank erosion and degraded aquatic habitat (Larsen et al. 1998).

Research on trampling effects in California grasslands has mainly occurred at the San Joaquin Experimental Range (SJER) in Fresno County (for a review see Menke 1989). Tate et al. (2004), working in the valley grassland/oak woodlands at SJER, found greater compaction in areas with moderate to heavy grazing intensities compared to historically ungrazed areas, indicating undesirable effects on soil physical properties. D'Antonio and Tyler (unpublished) found significantly increased bulk density within grazed compared to ungrazed (past 10 years) paddocks in Valley grasslands at Sedgwick reserve in Santa Barbara County with effects showing up to 30% more compaction in some grazed plots. Grazing was at moderate intensity and occurred only in the wet season.

Nutrient redistribution

Biogeochemical cycles are altered by grazing because herbivores mineralize organic matter and return it to the environment in solid, liquid, and gaseous forms (Allen et al. 1996, Hack-Ten-Broeke and Van Der Putten 1997, Oenema et al. 1997, Carran and Theobald 2000, Luo et al. 2000, Di and Cameron 2002, Anger et al. 2003). In general, grazing in grasslands accelerates carbon and nutrient cycling by effectively bypassing the microbial decomposition pathway (Ritchie et al. 1998, Singer and Schoenecker 2003). This acceleration happens in a spatially heterogenous manner because livestock use some areas preferentially and because their excreta is deposited in patches that are a small fraction of the grazed landscape (Tate et al. 2000, Tate et al. 2003).

Nitrogen quickly cycles within annual-dominated ecosystems (Woodmansee 1978, Jones and Woodmansee 1979, Woodmansee and Duncan 1980, Schimel et al. 1989, Davidson et al.

1990), where plant species possess low nutrient use efficiencies and high litter qualities irrespective of defoliation (Savelle 1977, Eviner 2004). In perennial grasslands of the Great Plains and the Upper Midwest, accelerated nutrient cycling as a result of livestock grazing is credited for stimulating net primary productivity (Frank and McNaughton 1993, Frank et al. 1994, Paine et al. 1999). However, grazing effects on nutrient dynamics in California annual grassland have not been observed (Davidson et al. 1993, Dahlgren et al. 1997, Herman et al. 2003).

Grazing effects on grassland productivity

Factors at many spatial and temporal scales interact to control herbaceous productivity in California's annual grasslands (Bartolome 1989). Aboveground biomass at late spring seed set varies interannually as a function of the timing and amount of precipitation and temperature (Talbot et al. 1939, Bentley and Talbot 1948, Heady 1958, George et al. 1988), and edaphic and topographic characteristics (Jackson et al. 1988, Callaway et al. 1991). A typical yearly production curve for annual grassland includes the onset of autumn germination with the first rains over 2.5 cm occurring within a one-week period (Figure 1). Slow winter growth progresses as temperatures decline, followed by rapid spring growth as soil temperatures increase concurrent with adequate soil moisture (Chiariello 1989). Peak standing crop of the herbaceous vegetation generally occurs between 1 April and 15 May followed by the death of the annual plants. Standing dead biomass slowly decomposes as summer drought slows microbial activity until the ensuing autumn rains stimulate decomposition concurrent with annual plant germination (Jackson et al. 1988).

The first concerted ecological research studies in the annual grassland were directed towards understanding the forage base for livestock grazing (Sampson 1917, Bentley and Talbot 1948, Sampson et al. 1951, Biswell 1956). Much of this work also established the primacy of location and weather as factors controlling herbaceous production and composition (Talbot et al. 1939, Heady 1958). Later studies and management practice have shown that the effects of grazing are related to the abundance of litter or residual dry matter (RDM, e.g. the senesced plant phytomass) remaining at the time of autumn germination (Hedrick 1948, Heady 1956, 1965, Bartolome et al. 1980, Bartolome et al. 2002). To maintain long-term livestock production in California annual grassland, range managers must cope with the vagaries of California climate. Bartolome et al. (1980) demonstrated that within a range of RDM levels representative of typical grazing intensities, RDM had a positive relationship to peak standing crop of the ensuing year (Fig. 2). This relationship was roughly general along a rainfall gradient from southern San Joaquin Valley to the northern Coast Ranges and has been validated for open annual grassland at a Sierran foothills site (Betts 2003). This relationship was weakest at sites with <20 cm total annual rainfall. Mechanisms for this relationship have not been elucidated but are believed to be a combination of favorable light, space, nutrient, and water modifications by moderate levels of RDM (Xiong and Nilsson 1997, 1999). The high RDM extreme (i.e. no defoliation), which was not tested by Bartolome et al. (1980), inhibited production on a Sierran foothill site (Bartolome et al. Submitted).

Belowground biomass responses to RDM were estimated by Betts (2003) who found that any aboveground defoliation treatment (i.e., 50, 100, or 150 g RDM·m⁻²) in open annual grassland increased the ensuing year's root:shoot biomass ratios (~0.8) compared to undefoliated controls (~0.5), which averaged 500 g RDM·m⁻². This root:shoot response is opposite to that

typically found in perennial grasslands in Continental climates where defoliation reduces root production (Turner et al. 1993, Johnson and Matchett 2001, Ferraro and Oesterheld 2002). To our knowledge, no other studies of belowground biomass responses to defoliation in California grasslands exist, reflecting past emphasis on production of available forage for livestock. The relatively recent emphasis on carbon sequestration in grassland soils to mitigate the accumulation of atmospheric greenhouse gases will likely stimulate belowground productivity research (Conant et al. 2001, Follett et al. 2001, Conant and Paustian 2002, Shaw et al. 2002, Dukes et al. 2005).

Grassland plant community responses to grazing

Species composition

In the 1950s and 1960s, UC Berkeley's Harold Heady conducted a series of experiments showing that fall RDM dramatically influenced biomass productivity and species composition in a high-rainfall ($89 \text{ cm}\cdot\text{y}^{-1}$) Mendocino County annual grassland site (Heady 1956, 1958, 1965). With no RDM at the time of germination, *Aira carophyllea*, *Baeria chrysostoma*, *Hypochoeris glabra*, and *Triphysaria eriantha* dominated the vegetation on the site. When plant residue was left on the ground, the relative cover of *Bromus hordeaceus* increased from 1 to 37% in 3 y; when all the mulch was removed each year, the cover of *B. hordeaceus* remained at < 2%. However, recent analysis of the species composition component of the Bartolome et al. (1980) dataset, which spanned 9 sites and 5 years, indicated that while some species may respond to RDM manipulations in some years, overall plant community composition is relatively insensitive to these changes (Jackson and Bartolome 2002). It is important to note that all of these studies used mowing rather than grazing to achieve RDM levels, which may bias results because grazing

is a selective process that is distributed over time, while mowing uniformly defoliates in pulse-like events.

We first classified plant communities from plots under a range of RDM treatments located along the latitudinal, hence rainfall, gradient indicated in Figure 2. Second, we used classification and regression tree (CART) analysis to examine the amount of deviance explained in interannual transitions amongst these communities. We found that about 60% of the deviance was attributable to location and weather patterns, <5% of the deviance was explained by the RDM gradient, and about 35% of the deviance was unexplained.

In these sites, composition seems to be entrained by annual weather patterns that appear to render overall community manipulation via livestock grazing futile. However, single species, such as a native perennial grass (Hatch et al. 1999, Bartolome et al. 2004), invasive plant (Thomsen et al. 1993, Betts 2003), or diversity (Meyer and Schiffman 1999) may still be managed by manipulating the timing, intensity, frequency, or duration of grazing as will be discussed below. RDM-based management prescriptions combined with manipulations of timing and intensity of grazing will need to be made and monitored on a site and time specific basis.

Plant species richness

Working in coast live oak savannas, Maranon and Bartolome (1994) showed plant species richness was higher under intermediate aboveground biomass levels compared to either lower or higher levels. These results follow the model of Grime (1979), which was discussed by Maranon and Garcia (1997), that hypothesizes a unimodal distribution of plant species richness along a productivity gradient. Maranon and Bartolome (1994) listed biomass levels for maximizing species diversity on California annual grassland/oak woodlands at 35 to 57 g

RDM·m⁻². Conversely, Bartolome et al. (2004) found no relationship between grazing intensity, measured as stocking rate, on diversity indices in perennial grass stands in the Coast Range. Fehmi and Bartolome (2002) showed that a possible tradeoff between livestock and rodent herbivory exists in these grasslands. In their study, rodents appeared to preferentially locate burrows (therefore disturb vegetation) in areas where livestock were excluded, i.e. high cover sites. This agrees with observational surveys by Stromberg and Griffin (1996) who demonstrated higher gopher activity in long ungrazed compared to grazed pastures in Monterey County. Hence, any response of plant species diversity to livestock grazing regime changes may be cancelled by rodent activity.

Harrison et al. (2003) examined effects of grazing and burning on richness in annual grasslands on serpentine and nonserpentine soils in the Coast Range north of San Francisco Bay. Grazing increased native plant diversity on the less productive serpentine soils, but not on the more productive nonserpentine soils. The authors of this study point out however, that grazing and burning effects were weak relative to extrinsic factors such as soil type. These results were validated by Safford and Harrison (2001) who also showed that higher plant diversity in grazed serpentine grasslands compared to serpentine roadside verges, which are typically ungrazed areas located between a road and a fence line. A follow-up survey of 92 sites on Valley Grassland of the northern Coast Range found that the presence or absence of grazing interacted with soil type and aspect in its effect on native and exotic plant species richness (Gelbard and Harrison 2003). Grazing was associated with lower native grass species diversity on non-serpentine soils, but did not affect the richness of native forb species. Conversely, less fertile serpentine soils supported greater native forb richness with grazing, but showed no effect of grazing for native grass richness.

In the wetter coastal prairie grasslands, a study of grazed and ungrazed sides of fencelines (Hayes and Holl 2003b) revealed that grazing was associated with a higher diversity of native annual forbs but also a higher richness of exotic annual species. Native perennial forbs showed decreased richness with grazing while exotic forbs increased with grazing. This study did not evaluate the role of other factors like soil type or aspect.

Grazing effects on particular taxa and functional groups

Native grasses and forbs

Most studies of grazing effects on native perennial grasses have emphasized the role of grazing in the demise of the putative dominant of the pre-Eurasian contact vegetation, *Nassella pulchra*. However, searching for edaphic and geographic correlates with *N. pulchra*, Bartolome and Gemmill (1981) rejected the notion that this species represents relictual dominance and hypothesized that it likely is a disturbance-adapted species that finds refuge in places where light is less limiting than belowground resources. In support of this, Dyer (2002) found that *N. pulchra* seed from grazed and/or burned individuals germinated and survived at higher rates than seed from undisturbed plants. Irrespective of its relictual status, many researchers have sought to determine management techniques, namely, combinations of grazing, burning, or grazing removal (Menke 1992, Hatch et al. 1999, Bartolome et al. 2004, Marty et al. 2005), that may enhance its abundance. Some of these studies indicated that *N. pulchra* was not especially tolerant of defoliation (Dennis 1989, Huntsinger et al. 1996, Marty et al. 2005). However, Dyer and Rice (1999) and Hamilton et al. (1999) demonstrated that *N. pulchra* is susceptible to competition from non-native species and when growing amongst non-native annual species it benefits from grazing because diffuse competition from these annuals is reduced (Dyer and Rice

1997, Malmstrom et al. 2006). Bartolome et al. (2004) working in Coast Range Grassland found a positive response of *Nassella pulchra* and *N. lepida* to a spring grazing treatment but only after the cessation of the treatment. These results indicate some positive residual effect of their seasonal grazing treatments that was magnified by removal of the disturbance. Many of the studies of *Nassella* spp responses to grazing stress the importance of climate variability in influencing their results and *Nassella* dynamics in general (Dyer et al. 1996, Merenlender et al. 2001, Bartolome et al. 2004, Marty et al. 2005).

California grasslands dominated by other perennial grass species, which are found mainly along the coast (i.e. Coastal Prairie), have received considerable attention recently (Stromberg and Griffin 1996, Hayes and Holl 2003b, Corbin et al. 2005). Working in three coastal prairie sites, Hayes and Holl (2003a) found that a gradient of defoliation intensity (clipping) reduced exotic grasses but had no effect on native perennial grasses including the common coastal prairie grass, *Danthonia californica*. This species was present in the previously discussed Bartolome et al. (2004) study plots and it increased with removal of livestock grazing. These results conflict with those of Hatch et al. (1999) and Biswell (1956), who found grazing removal decreased cover of *D. californica*. Likewise, in their extensive coastal fenceline survey Hayes and Holl (2003b) found ungrazed areas had lower cover of *D. californica* than grazed areas suggesting that this species benefits from grazing in at least some settings.

Several recent studies have evaluated the effects of grazing or clipping on native forbs. In a three-year clipping and mulch-removal study in the grassland of Carrizo Plain National Monument, San Luis Obispo County, Kimball and Schiffman (2003) found that clipping one to three times per growing season significantly reduced cover and species richness of native annual forbs and the native annual grass *Vulpia microstachys*. In contrast, non-native grass and forb

cover and species richness were largely unaffected by the simulated grazing. They speculated that Mediterranean grassland species, exposed to livestock grazing for many centuries, have adaptations such as compensatory growth that enable them to recover from grazing, while native species generally lack these mechanisms. In contrast to these results, grazing has been shown to favor native annual forbs in several other recent studies from other parts of California (Safford and Harrison 2001, Gelbard and Harrison 2003, Hayes and Holl 2003b, Marty 2005).

These varied and conflicting results indicate the importance of separating grazing effects on individuals, populations, and communities and the species-specific nature of grazing responses. If target perennial grasses are not already present on a site, no amount of grazing management or removal will encourage their abundance (Merenlender et al. 2001). This may also be true of some native annual forbs species, although seed bank limitation has not been tested for most forbs in California. If present on a site, native perennial grasses and native annual forbs have been shown to respond favorably to some disturbance treatments as discussed above. The particular combination of treatments depends on geography, soils, interspecific competition, and possibly weather patterns.

Non-native species

Little direct evidence exists that grazing promotes invasion of undesirable non-native plant species in California grasslands, though the 19th Century invasion of exotic annuals that now dominate occurred at the same time that livestock densities dramatically increased (Burcham 1957, Heady et al. 1992, Belsky and Gelbard 2000). Grazers may alter the competitive balance of natural communities by altering nutrient cycles and creating gaps for colonization—in effect, creating an alternate ecosystem more conducive to the invader (D'Antonio et al. 1999). But Levine et al.'s (2004) meta-analysis showed that herbivory by *native herbivores*

generally reduced colonization and spread of invasive species although most of their examples were from non-grassland communities dominated by native species. Of course, this ignores the fact that grazers, particularly large mammals, are excellent dispersal agents for plant species, whether they are invasive or not. Theory notwithstanding, little or no evidence linking grazing intensity to current plant invasion exists for California grasslands.

Yellow starthistle (*Centaurea solstitialis*) is a winter annual whose cover is expanding at an alarming rate on California rangelands. Gerlach and Rice (2003) determined that *C. solstitialis* colonized disturbed open patches more readily than its less invasive congeners. While grazing or defoliation were not explicitly examined, they inferred that grazing intensities that exposed bare ground would facilitate invasion and spread of this noxious species. Nonetheless *C. solstitialis* was less sensitive to competition from grasses than the congeners they also tested. Holmes and Rice (1997) and others (reviewed in Chapter 7) imply that winter annual grass dominance facilitates *C. solstitialis* invasion by creating an untapped pool of soil water that can be exploited by it with its summer active phenology. Whether grazing promoted the 19th century invasion of these annual grasses (that then promoted *C. solstitialis*) is a question that cannot be decisively answered. While *C. solstitialis* is relatively unpalatable and indeed is toxic to horses, Thomsen et al. (1993) showed that properly timed late spring/early summer intensive grazing by cattle or goats can be used as a tool to reduce cover and reproductive capacity of this species (and see Chapters. 20 and 24).

Betts (2003) found that the invasive annual barbed goatgrass (*Aegilops triuncialis*) was more likely to germinate and reach maturity in undisturbed plots than in plots with reduced RDM levels. In addition, *A. triuncialis* plants in ungrazed areas were more robust and produced more seeds than those goatgrass plants in grazed areas. Seedheads in grazed areas experienced

significant predation by granivorous rodents, and the high amount of RDM in the ungrazed areas also may have created a more favorable micro-environment for *A. triuncialis*. While grazing may not be able to control *A. triuncialis* directly (goatgrass is unpalatable to livestock), grazed areas may be under lower threat of goatgrass establishment than ungrazed areas.

Medusahead (*Taeniatherum caput-medusae*) is another annual grass that is a significant pest in grazed grasslands of California because of its low palatability and nutritional quality for livestock (Young 1992, Betts 2003). This grass has been estimated to reduce grazing capacity by 40 to 75% (Major et al. 1960). While sheep will not eat silage containing medusahead (Bovey et al. 1961), they will eat medusahead plants if they are young (Lusk et al. 1961) such that moderate-intensity, early-season grazing may reduce medusahead cover (Cooper 1960). Results from the studies cited above illustrate the importance of grassland management based upon scientifically produced information that is applicable to appropriate sites, scales, and taxa. Grazing managers control animal type, intensity, frequency, and duration of grazing, therefore grazing effects should not be assessed as an “either-or” proposition.

Grazing effects in grassland landscapes

Thus far we have treated grazing effects on California grasslands as though the grasslands are very discrete, uniform units. However, these communities grade more or less strongly into oak savanna and woodland (Allen-Diaz et al. 1997). Riparian zones are nested within these landscapes forming corridors and patches of mainly perennial vegetation. Virtually all of California’s drinking water passes through annual grassland and oak woodland ecosystems (Tate et al. 1999), which are predominantly managed with grazing (McClaran and Bartolome 1985, Standiford and Tinnin 1996). Suburban development within these rangelands places

increasing pressure on management agencies to reduce wildfire fuel loads (Fried and Huntsinger 1998). On the steep terrain of California's annual grassland/oak woodland watersheds, grazing and prescribed fire are the most feasible vegetation management options (Stephens and Ruth 2005). Hence, a watershed-level approach to understanding how grazing affects water quantity and quality is critical to managing these landscapes. The importance of the watershed level of organization notwithstanding, at this time only a single controlled and replicated paired-watershed experiment is underway to understand grazing and burning effects on water quantity and quality as well as vegetation dynamics at this scale (Dahlgren et al. 2001). Recent work showed that nitrate pulses in streams draining large Sierra Nevada watersheds were mainly the result of sedimentary rock weathering (Holloway et al. 1998), which demonstrates the importance of carefully separating management effects from "background" contributions to water quality (Tate et al. 1999). Experimental work at this scale will require long-term (decadal) datasets where temporal and spatial variability can be separated from management signals (sensu Lewis et al. 2000, Jackson and Allen-Diaz 2006).

Grazing dynamics modulated by the presence of oak canopy

Dahlgren et al. (1997) described soils beneath oak canopy as "islands of fertility" because of greater carbon, nitrogen, and phosphorus stocks compared to adjacent open grasslands sites. The patchiness of oak woodland canopy may be enhanced by the ability of oaks to garner water and nutrients from beyond the canopy perimeter, from the open grassland spaces between them and their neighbors, and then preferentially returning leaf litter below the existing canopy. If this model holds, it would constitute a redistribution of ecosystem resources within the savanna landscape (sensu Schlesinger and Pilmanis 1998, Cross and Schlesinger 1999, Huenneke et al. 2002). However, this process would constitute a positive feedback that is theoretically

unsustainable in the long-term, depressing herbaceous production in the open (assuming no nitrogen fixation in the open), but this effect has not been observed. An untested hypothesis is that herbivores provide a check on this effect by harvesting herbaceous resources from beneath the canopy and redistributing them in a more homogeneous way across the landscape.

Herbaceous understory production is primarily controlled by interannual weather variability, however, several workers have demonstrated that tree canopy cover exerts a strong but variable, influence on peak standing biomass depending on regional location, tree density, and tree type (Frost and McDougald 1989, Callaway et al. 1991, Ratliff et al. 1991, Bartolome et al. 1994). Relative to open grasslands, canopy cover inhibits herbaceous production in areas of California receiving >50 cm annual precipitation (McClaran and Bartolome 1989). The inverse relationship generally holds for drier portions of the state where canopy cover attenuates drought stress. However, Callaway et al. (1991) showed experimentally that within-site variation in the affect of an oak canopy was related to shallow, fine root abundance of oaks (and see chapter 12). High oak fine root biomass suppressed herb production while low oak fine root biomass promoted herb biomass exceeding that measured in adjacent open grassland. From a livestock production perspective, Frost et al. (1991) found that an increase in tissue and litter quality per unit biomass under oak canopy in drier regions more than compensated for any reduction in herbage mass from the canopy cover. Nutrient concentrations differed as a result of species composition differences rather than some change in individual plant nutrient use efficiencies.

Herbaceous riparian zones nested within grasslands

High intensity grazing can negatively affect water quality, plant biodiversity, productivity, wildlife habitat, wildlife species biodiversity, and nutrient cycling in riparian areas in regions with Continental-type climates (Kauffman et al. 1983a,b Kauffman and Krueger 1984,

Fleischner 1994, Clary 1995, 1999). However, extrapolation of these results to Mediterranean-type regions should be made very cautiously (Larsen et al. 1998, Gasith and Resh 1999). Effects of moderate to light grazing on ecosystems of these regions tend to be overwhelmed by larger scale environmental fluctuations.

Nested within annual grasslands are riparian zones where relatively little scientific study about grazing effects has occurred in California. Riparian zones provide many important ecosystem services (Naiman and Decamps 1997, Sabater et al. 2000), which may be modified by livestock grazing or its cessation. Much of the water exiting grassland watersheds passes through the highly productive plant communities that are situated at the terrestrial-aquatic interface (Huang 1997, Tate et al. 1999, Lewis et al. 2000). Wetland vegetation in these zones, typically cattail (*Typha* spp.), sedges, rushes, and perennial grasses, may act as nutrient filters (primarily nitrate) as waters emerge at the soil surface. Jackson et al. (2006) determined with a paired-plot grazing removal experiment that nitrate concentrations in surface waters where grazing was removed for only two years were as much as five times greater than grazed counterparts, these concentrations far exceeded the US-EPA maximum standard for surface waters of 10 ppm NO₃-N (Fan et al. 1987). They speculated that reduced herbaceous production that resulted from litter accumulation under grazing removal led to reduced plant N demand, hence greater throughput of nitrate to the downstream aquatic ecosystem.

Spring-fed wetlands and first-order riparian areas are often the only sources of surface water in grasslands and are especially heavily utilized by grazing animals. However, light to moderate, autumn/winter grazing had little effect on Sierra Nevada foothill spring-fed vegetation after 6 years of treatment (Allen-Diaz and Jackson 2000). Continued monitoring of these systems under experimental treatments showed that by years 7 through 10, moderate grazing

reduced herbaceous cover, light grazing had minimal effect, and grazing removal significantly increased cover (Jackson and Allen-Diaz 2006). Furthermore, the long-term results from this study demonstrated that the riparian creeks emanating from the more marshy wetlands where spring waters emerge display dynamics that were fundamentally different, i.e. equilibrium community dynamics, than the nonequilibrium response exhibited in their upslope marshy spring counterparts (Fig. 3).

Equilibrium dynamics were observed by Marty (2005) for vernal pools in the Valley Grassland whose endemic, diverse, largely annual flora is deleteriously affected by the removal of livestock grazing. In this work, three years of grazing removal resulted in higher cover of exotic annual grasses and lower cover and richness of native species in vernal pool edges compared to grazed pool edges. Species in the pool bottoms did not respond to grazing regime manipulations. Further, species richness of aquatic invertebrates declined when livestock grazing was removed from pools. Marty also found that the upland grassland species between the pools responded similarly to grazing as the pool edge species: native species richness and cover increased with grazing. The grazing regime producing the strongest response was continuous grazing (contrasted with wet season and dry season grazing). Marty argues that these pool assemblages evolved in the presence of large herds of tule elk which possibly explains their current positive responses to grazing.

Livestock production grazing management decisions are usually made at the landscape level based on the matrix vegetation (annual grassland in this case), but nested ecosystems, such as herb dominated vernal pools, spring-fed wetlands and creeks, may respond differentially requiring a more nuanced approach that includes site specific information relevant to management goals.

Wildlife grazing and grazing effects on wildlife

Most literature treating grazing in California focuses on the productivity and composition of annual grasslands under livestock grazing because this is the dominant land-use of California rangelands (Huntsinger et al. 1997). However, a growing appreciation and understanding of wildlife grazers, such as elk, deer, and small mammals is apparent in the literature (Lidicker 1989, Hobbs and Mooney 1995, Fehmi and Bartolome 2002, Eviner and Chapin 2003, 2005). Schiffman (Ch. 13) provides a thorough review of small mammal herbivory effects on the structure and function of California grasslands.

Animals are known to graze selectively—they choose certain plants over others—but the impacts of selection have not been well-linked to observed changes in the plant community or productivity (Bartolome 1993). Of the modern large grassland herbivores, cattle, horses, and tule elk tend to prefer grasses (McCullough 1969, Heady and Child 1994), while sheep (Bartolome and McClaran 1992) and deer (Gogan and Barrett 1995) prefer forbs. Antelope, which were formerly widespread in the grassland but are now highly localized, are opportunistic and prefer grasses, forbs, or shrubs depending on the season (Yoakum and O'Gara 2000). Elk also change their diet seasonally preferring forbs in the spring and summer and grasses in the fall and winter (Gogan and Barrett 1995).

Although native grazers and livestock differ in dietary preference there is considerable overlap (Elliott and Barrett 1985). Recent work by Johnson and Cushman (Johnson and Cushman, in press) demonstrated that *removal* of tule elk grazing from Coastal Prairie dramatically decreased annual plant cover, while increasing some perennial grasses (e.g. the invasive *Holcus lanatus*) and having no effect on others. These results point to the importance of selective defoliation in perennial grasslands, which is likely to alter competitive interactions

among functional groups. However, when only one functional group is present, as is the case with many annual grasslands, grazing effects on composition are difficult to detect. Given the importance of RDM at autumn germination on plant productivity and the nominal or highly variable effect of grazing on community structure, there is no reason to expect wildlife grazing would impart any different effect on annual grasslands than livestock unless their patterns of seasonal use are strongly different. Their effect on productivity should be mediated by grazing intensity similar to livestock.

The effects of grazing on several key wildlife taxa are listed in Barry et al. (2006). This publication attempts to decompose the interacting effects of grazing animal type, intensity, and season on the following: California Ground Squirrel, Burrowing Owl, Kit Fox, Bay Checkerspot Butterfly, Smith's Blue Butterfly, Steelhead Trout, California Quail, and Tiger Salamander. The numerous and varied interactions that make such an approach necessary preclude their exposition here. This and similar publications should prove useful for managers struggling with multiple, often conflicting, management goals and objectives. Posting and updating of these efforts on the internet should allow them to be used opportunistically and adaptively—two key characteristics for management of highly variable nonequilibrium systems (Westoby et al. 1989).

Summary

Grazing in Californian grasslands has occurred for millenia, but domestic livestock have grazed for only about 250 years. The introduction of domesticated livestock corresponded with a massive conversion from some more or less unknown past flora to one dominated by annual grasses and forbs native to the Mediterranean region. Grazing research in California was initiated early in the 20th Century. The main response variables during the majority of the

century were forage production and species composition. This research resulted in a useful management model for livestock production, manipulation of residual dry matter (RDM), because a simple linear relationship between RDM and ensuing year's production was roughly generalizable across the State's annual grasslands. While many have speculated on the mechanisms underlying this relationship—e.g. favorable modification of temperature, moisture, soil protection, nitrogen availability—they have not been uncovered experimentally. Little literature exists assessing grazing effects on California grassland nitrogen cycling, decomposition, or belowground productivity.

Early range managers understood that intra- and inter-annual floristic variability was dominated by weather patterns. Nonetheless, many sought to understand species composition in annual grasslands as a function of grazing management because the assumption of equilibrium community dynamics, which were prevalent in the Great Plains and the Midwest (Clements 1936, Dyksterhuis 1949), dictated that plant-herbivore dynamics exert primary control on the plant community. The slow realization that nonequilibrium dynamics prevail in California and other arid and semi-arid grasslands indicates that empirical approaches to understanding plant community responses to grazing are necessary because they are data-driven, flexible, and allow for contingent effects of weather, geography, and history to be assessed (Allen-Diaz and Bartolome 1998). Similarly, site and time specific data are beginning to show that grazing can be effectively applied as a tool for native grass enhancement, invasive species control, fuel load reduction, and habitat management. Maintenance or restoration of ecosystem services in California grasslands demands a watershed-level understanding of grazing effects, which is sorely lacking at this time.

Grazing managers in California's mediterranean climate should not expect to realize narrowly defined outcomes, especially when considering species composition. Instead, a range of possible results should be anticipated. If we have learned anything about California's nonequilibrium grasslands, it is that the response of the system to grazing depends on when and where we observe the response.

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Literature cited

- Allen, A. G., S. C. Jarvis, and D. M. Headon. 1996. Nitrous oxide emissions from soils due to inputs of nitrogen from excreta return by livestock on grazed grassland in the UK. *Soil Biology & Biochemistry* **28**:597-607.
- Allen-Diaz, B., and J. W. Bartolome. 1998. Sagebrush-grass vegetation dynamics: comparing classical and state-transition models. *Ecological Applications* **8**:795-804.
- Allen-Diaz, B., and R. D. Jackson. 2000. Grazing effects on spring ecosystem vegetation of California's hardwood rangelands. *Journal of Range Management* **53**:215-220.
- Allen-Diaz, B., R. D. Jackson, and J. S. Fehmi. 1998. Detecting channel morphology change in California's hardwood rangeland spring ecosystems. *Journal of Range Management* **51**:514-518.
- Allen-Diaz, B. H., J. W. Bartolome, and M. P. McClaran. 1997. California Oak Savanna. Pages 322-339 in R. C. Anderson, J. S. Fralish, and J. M. Baskin, editors. *Savanna, Barren and Rock Outcrop Plant Communities of North America*. Cambridge University Press, Cambridge.
- Anger, M., C. Hoffmann, and K. U. W. 2003. Nitrous oxide emissions from artificial urine patches applied to different N-fertilized swards and estimated annual N₂O emissions for differently fertilized pastures in an upland location in Germany. *Soil Use & Management* **19**:104-111.
- Axelrod, D. I. 1944. The Oakdale flora. Carnegie Institute Washington Publication **553**:147-166.
- Barry, S., R. E. Larsen, G. A. Nader, M. Doran, K. Guenther, and G. Hayes. 2006. Understanding livestock grazing impacts: strategies for the California annual grassland and oak woodland vegetation series. Publication 21626, University of California Division of Agriculture and Natural Resources, Oakland.
- Bartolome, J. W. 1979. Germination and seedling establishment in California annual grassland. *Journal of Ecology* **67**:273-281.
- Bartolome, J. W. 1989. Local temporal and spatial structure. Pages 73-77 in L. F. Huenneke and H. A. Mooney, editors. *Grassland structure and function: California annual grassland*. Kluwer Academic Publishers, Boston.
- Bartolome, J. W. 1993. Application of herbivore optimization theory to rangelands of the western United States. *Ecological Applications* **3**:27-29.
- Bartolome, J. W., B. H. Allen-Diaz, and W. D. Tietje. 1994. The effect of *Quercus douglasii* removal on understory yield and composition. *Journal of Range Management* **47**:151-154.

- Bartolome, J. W., W. J. Barry, T. Griggs, and P. Hopkinson. In press. Valley grassland. *in* M. G. Barbour, editor. Terrestrial vegetation of California. UC Press, Berkeley.
- Bartolome, J. W., J. S. Fehmi, R. D. Jackson, and B. Allen-Diaz. 2004. Response of a native perennial grass stand to disturbance in California's Coast Range Grassland. *Restoration Ecology* **12**:279-289.
- Bartolome, J. W., W. E. Frost, N. K. McDougald, and J. M. Connor. 2002. California guidelines for residual dry matter (RDM) management on coastal and foothill annual rangelands. Publication 8092, Division of Agricultural and Natural Resources, University of California.
- Bartolome, J. W., and B. Gemmill. 1981. The ecological status of *Stipa pulchra* (Poaceae) in California. *Madroño* **28**:172-184.
- Bartolome, J. W., R. D. Jackson, A. D. K. Betts, J. M. Connor, G. A. Nader, and K. W. Tate. Submitted. Residual dry matter effects on California annual rangeland composition and production. *Rangeland Ecology & Management*.
- Bartolome, J. W., and M. P. McClaran. 1992. Composition and production of California oak savanna seasonally grazed by sheep. *Journal of Range Management* **45**:103-107.
- Bartolome, J. W., M. C. Stroud, and H. F. Heady. 1980. Influence of natural mulch on forage production on differing California annual range sites. *Journal of Range Management* **33**:4-8.
- Beetle, A. A. 1947. Distribution of the native grasses of California. *Hilgardia* **17**:309-357.
- Begon, M., J. L. Harper, and C. R. Townsend. 1996. *Ecology: individuals, populations, and communities*, 3rd edition. Blackwell Science, Oxford, UK.
- Belsky, A. J., and J. L. Gelbard. 2000. *Livestock grazing and weed invasions in the arid West*. Oregon Natural Desert Association, Bend, OR.
- Bentley, J. R., and M. W. Talbot. 1948. Annual-plant vegetation of the California foothills as related to range management. *Ecology* **29**:72-79.
- Betts, A. D. K. 2003. Ecology and control of goatgrass (*Aegilops triuncialis*) and medusahead (*Taeniatherum caput-medusae*) in California annual grasslands. PhD dissertation. University of California, Berkeley, Berkeley.
- Biswell, H. H. 1956. Ecology of California grasslands. *Journal of Range Management* **9**:19-24.
- Bond, W. J., F. I. Woodward, and G. F. Midgley. 2005. The global distribution of ecosystems in a world without fire. *New Phytologist* **165**:525-537.
- Bovey, R., D. L. Tourneau, and L. C. Erickson. 1961. The chemical composition of medusahead and downy brome. *Weeds* **9**:307-311.

- Briske, D. D. 1991. Developmental morphology and physiology of grasses. Pages 85-108 *in* R. K. Heitschmidt and J. W. Stuth, editors. *Grazing management: An ecological perspective*. Timber Press, Portland, OR.
- Burcham, L. 1957. *California range land: an historico-ecological study of the range resources of California*. Division of Forestry, Department of Natural Resources, State of California, Sacramento, CA.
- Burcham, L. T. 1975. Climate, structure, and history of California's annual grassland ecosystem. Pages 16-34 *in* R. M. Love, editor. *The California Annual Grassland Ecosystem*. Institute of Ecology, University of California, Davis.
- Callaway, R. M., N. M. Nadkarni, and B. E. Mahall. 1991. Facilitation and interference of *Quercus douglasii* on understory productivity in central California. *Ecology* **72**:1484-1499.
- Carran, R. A., and P. W. Theobald. 2000. Effects of excreta return on properties of a grazed pasture soil. *Nutrient Cycling in Agroecosystems* **56**:79-85.
- Chiariello, N. R. 1989. Phenology of California grasslands. Pages 47-58 *in* L. F. Huenneke and H. A. Mooney, editors. *Grassland structure and function: California annual grassland*. Kluwer Academic Publishers, Boston.
- Clary, W. P. 1995. Vegetation and soil responses to grazing simulation on riparian meadows. *Journal of Range Management* **48**:18-25.
- Clary, W. P. 1999. Stream channel and vegetation responses to late spring cattle grazing. *Journal of Range Management* **52**:218-227.
- Clements, F. E. 1934. The relict method in dynamic ecology. *Journal of Ecology* **22**:39-68.
- Clements, F. E. 1936. Nature and structure of the climax. *Journal of Ecology* **24**:252-284.
- Conant, R. T., and K. Paustian. 2002. Potential soil carbon sequestration in overgrazed grassland ecosystems. *Global Biogeochemical Cycles* **16**.
- Conant, R. T., K. Paustian, and E. T. Elliott. 2001. Grassland management and conversion into grassland: effects on soil carbon. *Ecological Applications* **11**:343-355.
- Cooper, D. W. 1960. Fort Baker ranges return to champagne grasses. *Journal of Range Management* **13**:203-205.
- Corbin, J. D., M. A. Thomsen, T. E. Dawson, and C. M. D'Antonio. 2005. Summer water use by California coastal prairie grasses: fog, drought, and community composition. *Oecologia* **145**:511-521.
- Cross, A. F., and W. H. Schlesinger. 1999. Plant regulation of soil nutrient distribution in the northern Chihuahuan Desert. *Plant Ecology* **145**:11-25.

- Dahlgren, R. A., M. J. Singer, and X. Huang. 1997. Oak tree and grazing impacts on soil properties and nutrients in a California oak woodland. *Biogeochemistry* **39**:45-64.
- Dahlgren, R. A., K. W. Tate, D. Lewis, E. R. Atwill, J. M. Harper, and B. Allen-Diaz. 2001. Watershed research examines rangeland management effects on water quality. *California Agriculture* **55**:64-71.
- Damhoureyeh, S. A., and D. C. Hartnett. 2002. Variation in grazing tolerance among three tallgrass prairie plant species. *American Journal of Botany* **89**:1634-1643.
- Daniel, J. A., K. Potter, W. Altom, H. Aljoe, and R. Stevens. 2002. Long-term grazing density impacts on soil compaction. *Transactions of the Asae* **45**:1911-1915.
- D'Antonio, C. M., T. L. Dudley, and M. Mack. 1999. Disturbance and biological invasions: direct effects and feedbacks. *in* L. R. Walker, editor. *Ecosystems of disturbed ground*. Elsevier, New York.
- Davidson, E. A., D. J. Herman, A. Schuster, and M. K. Firestone. 1993. Cattle grazing and oak trees as factors affecting soil emissions of nitric oxide from an annual grassland. Pages 100-119 *in* L. A. Harper, G. Peterson, P. S. Baenziger, and R. J. Luxmoore, editors. *Agricultural ecosystem effects on trace gases and global climate change: proceedings of a symposium*. ASA special publication no. 55. American Society of Agronomy: Crop Science Society of America: Soil Science Society of America, Madison, WI.
- Davidson, E. A., J. M. Stark, and M. K. Firestone. 1990. Microbial production and consumption of nitrate in an annual grassland. *Ecology* **71**:1968-1975.
- Del-Val, E. K., and M. J. Crawley. 2005. Are grazing increaser species better tolerators than decreasers? An experimental assessment of defoliation tolerance in eight British grassland species. *Journal of Ecology* **93**:1005-1016.
- Dennis, A. 1989. Effects of defoliation on three native perennial grasses in the California annual grassland. PhD dissertation. University of California, Berkeley.
- Di, H. J., and K. C. Cameron. 2002. Nitrate leaching in temperate agroecosystems: sources, factors and mitigating strategies. *Nutrient Cycling in Agroecosystems* **64**:237-256.
- Dukes, J. S., N. R. Chiariello, E. E. Cleland, L. A. Moore, M. R. Shaw, S. Thayer, T. Tobeck, H. A. Mooney, and C. B. Field. 2005. Responses of grassland production to single and multiple global environmental changes. *Plos Biology* **3**:1829-1837.
- Dyer, A. R. 2002. Burning and grazing management in a California grassland: effect on bunchgrass seed viability. *Restoration Ecology* **10**:107-111.
- Dyer, A. R., and K. J. Rice. 1997. Intraspecific and diffuse competition: the response of *Nassella pulchra* in a California grassland. *Ecological Applications* **7**:484-492.

- Dyer, A. R., and K. J. Rice. 1999. Effects of competition on resource availability and growth in a California bunchgrass. *Ecology* **80**:2697-2710.
- Dyer, M. I., C. L. Turner, and T. R. Seastedt. 1993. Herbivory and its consequences. *Ecological Applications* **3**:10-16.
- Dyksterhuis, E. J. 1949. Condition and management of rangeland based quantitative ecology. *Journal of Range Management* **2**:104-115.
- Edwards, S. W. 1992. Observations on the prehistory and ecology of grazing in California. *Fremontia* **20**:3-11.
- Edwards, S. W. 1996. A Rancholabrean-age latest-Pleistocene bestiary for California botanists. *Four Seasons* **10**:5-34.
- Elliott, H. W., and R. H. Barrett. 1985. Dietary overlap among Axis, Fallow, and Blacktailed deer and cattle. *Journal of Range Management* **38**:546-550.
- Eviner, V. T. 2004. Plant traits that influence ecosystem processes vary independently among species. *Ecology* **85**:2215-2229.
- Eviner, V. T., and F. S. Chapin. 2003. Gopher-plant-fungal interactions affect establishment of an invasive grass. *Ecology* **84**:120-128.
- Eviner, V. T., and F. S. Chapin. 2005. Selective gopher disturbance influences plant species effects on nitrogen cycling. *Oikos* **109**:154-166.
- Ewing, R. A., N. Tosta, R. Tuazon, L. Huntsinger, R. Morose, K. Nielson, R. Motroni, and S. Turan. 1988. California's forests and rangelands: Growing conflict over changing uses. California Dept. of Forestry and Fire Protection, Forest and Rangeland Resources Assessment Program, Sacramento, CA.
- Fan, A. M., C. C. Willhite, and S. A. Book. 1987. Evaluation of the nitrate drinking water standard with reference to infant methemoglobinemia and potential reproductive toxicity. *Regulatory Toxicology and Pharmacology* **7**:135-148.
- Fehmi, J. S., and J. W. Bartolome. 2002. Species richness and California voles in an annual and a perennial grassland. *Western North American Naturalist* **62**:73-81.
- Ferraro, D. O., and M. Oesterheld. 2002. Effect of defoliation on grass growth. A quantitative review. *Oikos* **98**:125-133.
- Fleischner, T. L. 1994. Ecological costs of livestock grazing in western North America. *Conservation Biology* **8**:629-644.
- Follett, R. F., J. M. Kimble, and R. Lal. 2001. The potential of U.S. grazing lands to sequester carbon and mitigate the greenhouse effect. Lewis Publishers, New York.

- Frank, D. A., R. S. Inouye, N. Huntly, G. W. Minshall, and J. E. Anderson. 1994. The biogeochemistry of a north-temperate grassland with native ungulates: Nitrogen dynamics in Yellowstone National Park. *Biogeochemistry* **26**:163-188.
- Frank, D. A., and S. J. McNaughton. 1993. Evidence for the promotion of aboveground grassland production by native large herbivores in Yellowstone National Park. *Oecologia* **96**:157-161.
- Fried, J., and L. Huntsinger. 1998. Managing for naturalness at Mt. Diablo State Park. *Society and Natural Resources* **11**:505-516.
- Frost, W. E., and N. K. McDougald. 1989. Tree canopy effects on herbaceous production of annual rangeland during drought. *Journal of Range Management* **42**:281-283.
- Frost, W. E., N. K. McDougald, and M. W. Demment. 1991. Blue oak canopy effect on seasonal forage production and quality. Pages 307-311 in R. Standiford, editor. Proceedings of the symposium on oak woodlands and hardwood rangeland management. GTR-PSW-126, Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, Davis, CA.
- Gasith, A., and V. H. Resh. 1999. Streams in Mediterranean climate regions: abiotic influences and biotic responses to predictable seasonal events. *Annual review of Ecology and Systematics* **30**:51-81.
- Gelbard, J. L., and S. Harrison. 2003. Roadless habitats as refuges for native grasslands: Interactions with soil, aspect, and grazing. *Ecological Applications* **13**:404-415.
- George, M. R., R. E. Larsen, N. K. McDougald, K. W. Tate, J. D. Gerlach, and K. O. Fulgham. 2002. Influence of grazing on channel morphology of intermittent streams. *Journal of Range Management* **55**:551-557.
- George, M. R., C. A. Raguse, W. J. Clawson, C. B. Wilson, R. T. Willoughby, N. K. McDougald, D. A. Duncan, and A. H. Murphy. 1988. Correlation of degree-days with annual herbage yields and livestock gains. *Journal of Range Management* **41**:193-196.
- Gerlach, J. D., and K. J. Rice. 2003. Testing life history correlates of invasiveness using congeneric plant species. *Ecological Applications* **13**:167-179.
- Gogan, P. J. P., and R. H. Barrett. 1995. Elk and deer diets in a coastal prairie-scrub mosaic, California. *Journal of Range Management* **48**:327-335.
- Grime, J. P. 1979. *Plant strategies and vegetation processes*. Wiley, New York.
- Hack-Ten-Broeke, M. J. D., and A. H. J. Van Der Putten. 1997. Nitrate leaching affected by management options with respect to urine-affected areas and groundwater levels for grazed grassland. *Agriculture Ecosystems & Environment* **66**:197-210.

- Hamilton, J. G. 1998. Changing perceptions of pre-European grasslands in California. *Madroño* **44**:311-333.
- Hamilton, J. G., C. Holzapfel, and B. E. Mahall. 1999. Coexistence and interference between a native perennial grass and non-native annual grasses in California. *Oecologia* **121**:518-526.
- Harrison, S., B. D. Inouye, and H. D. Safford. 2003. Ecological heterogeneity in the effects of grazing and fire on grassland diversity. *Conservation Biology* **17**:837-845.
- Hatch, D. A., J. W. Bartolome, J. S. Fehmi, and D. S. Hillyard. 1999. Effects of burning and grazing on a coastal California grassland. *Restoration Ecology* **7**:376-381.
- Hayes, G. F., and K. D. Holl. 2003a. Cattle grazing impacts on annual forbs and vegetation composition of mesic grasslands in California. *Conservation Biology* **17**:1694-1702.
- Hayes, G. F., and K. D. Holl. 2003b. Site-specific responses of native and exotic species to disturbances in a mesic grassland community. *Applied Vegetation Science* **6**:235-244.
- Heady, H. F. 1956. Changes in a California annual plant community induced by manipulation of natural mulch. *Ecology* **37**:798-912.
- Heady, H. F. 1958. Vegetational changes in the California annual type. *Ecology* **39**:402-416.
- Heady, H. F. 1965. The influence of mulch on herbage production in an annual grassland. *Proceedings of the 9th International Grassland Congress* **1**:391-394.
- Heady, H. F. 1977. Valley grassland. Pages 491-513 in M. G. Barbour and J. Major, editors. *Terrestrial vegetation of California*. John Wiley & Sons, Inc, New York.
- Heady, H. F., J. W. Bartolome, M. D. Pitt, G. D. Savelle, and M. C. Stroud. 1992. California prairie. Pages 313-332 in R. T. Coupland, editor. *Natural grasslands*. Elsevier, New York, N.Y.
- Heady, H. F., and R. D. Child. 1994. *Rangeland ecology and management*. Westview Press, Boulder.
- Hedrick, D. W. 1948. The mulch layer of California annual ranges. *Journal of Range Management* **1**:22-25.
- Heitschmidt, R. K., and J. W. Stuth. 1991. *Grazing management: an ecological perspective*. Timber Press, Portland, OR.
- Herman, D. J., L. J. Halverson, and M. K. Firestone. 2003. Nitrogen dynamics in an annual grassland: oak canopy, climate, and microbial population effects. *Ecological Applications* **13**:593-604.

- Hik, D. S., and R. L. Jefferies. 1990. Increases in the net aboveground primary production of a salt-marsh forage grass - a test of the predictions of the herbivore-optimization model. *Journal of Ecology* **78**:180-195.
- Hobbs, R. J., and H. A. Mooney. 1995. Spatial and temporal variability in California annual grassland: Results from a long-term study. *Journal of Vegetation Science* **6**:43-56.
- Holland, E. A., W. J. Parton, J. K. Detling, and D. L. Coppock. 1992. Physiological responses of plant populations to herbivory and their consequences for ecosystem nutrient flow. *The American Naturalist* **140**:685-706.
- Holloway, J. M., R. A. Dahlgren, B. Hansen, and W. H. Casey. 1998. Contribution of bedrock nitrogen to high nitrate concentrations in stream water. *Nature* **395**:785-788.
- Holstein, G. 2001. Pre-agricultural grassland in central California. *Madrono* **48**:253-264.
- Huang, X. 1997. Watershed hydrology, soil, and biogeochemistry in an oak woodland annual grassland ecosystem in the Sierra Foothills, California. Ph.D. dissertation. University of California, Davis.
- Huenneke, L. F., J. P. Anderson, M. Remmenga, and W. H. Schlesinger. 2002. Desertification alters patterns of aboveground net primary production in Chihuahuan ecosystems. *Global Change Biology* **8**:247-264.
- Huntsinger, L., L. Buttolph, and P. Hopkinson. 1997. Ownership and management changes on California hardwood rangelands: 1985 to 1992. *Journal of Range Management* **50**:423-430.
- Huntsinger, L., M. P. McClaran, A. Dennis, and J. W. Bartolome. 1996. Defoliation response and growth of *Nassella pulchra* (A. Hitchc.) Barkworth from serpentine and non-serpentine populations. *Madrono* **43**:46-57.
- Jackson, L. E., R. B. Strauss, M. K. Firestone, and J. W. Bartolome. 1988. Plant and soil nitrogen dynamics in California annual grassland. *Plant and Soil* **110**:9-17.
- Jackson, R. D., and B. Allen-Diaz. 2006. Spring-fed wetland and riparian plant communities respond differently to altered grazing intensity. *Journal of Applied Ecology* **43**:485-498.
- Jackson, R. D., B. Allen-Diaz, L. G. Oates, and K. W. Tate. 2006. Grazing removal increases spring-fed wetland nitrate concentrations in a Californian oak savanna. *Ecosystems* **9**:1-15.
- Jackson, R. D., and J. W. Bartolome. 2002. A state-transition approach to understanding nonequilibrium plant community dynamics of California grasslands. *Plant Ecology* **162**:49-65.
- Janis, C. M., J. Damuth, and J. M. Theodora. 2002. The origins and evolution of the North American grassland biome: the story from the hoofed mammals. *Palaeogeography Palaeoclimatology Palaeoecology* **177**:183-198.

- Johnson, B. E., and J. H. Cushman. In press. Influence of a large herbivore reintroduction on plant invasions and community composition in a California grassland.
- Johnson, L. C., and J. R. Matchett. 2001. Fire and grazing regulate belowground processes in tallgrass prairie. *Ecology* **82**:3377-3389.
- Jones, M. B., and R. G. Woodmansee. 1979. Biogeochemical cycling in annual grassland ecosystems. *Botanical Review* **45**:111-114.
- Kauffman, J. B., and W. C. Krueger. 1984. Livestock impacts on riparian ecosystems and streamside management implications: a review. *Journal of Range Management* **37**:430-438.
- Kauffman, J. B., W. C. Krueger, and M. Vavra. 1983a. Effects of late season cattle grazing on riparian plant communities. *Journal of Range Management* **36**:685-691.
- Kauffman, J. B., W. C. Krueger, and M. Vavra. 1983b. Impacts of cattle on streambanks in northeastern Oregon. *Journal of Range Management* **36**:683-685.
- Kimball, S., and P. M. Schiffman. 2003. Differing effects of cattle grazing on native and alien plants. *Conservation Biology* **17**:1681-1693.
- Knapp, A. K., J. M. Blair, J. M. Briggs, S. L. Collins, D. C. Hartnett, L. C. Johnson, and E. G. Towne. 1999. The keystone role of bison in north American tallgrass prairie - Bison increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem processes. *Bioscience* **49**:39-50.
- Larsen, R. E., W. C. Krueger, M. R. George, M. R. Barrington, J. C. Buckhouse, and D. E. Johnson. 1998. Viewpoint: livestock influences on riparian zones and fish habitat: Literature classification. *Journal of Range Management* **51**:661-664.
- Lemaire, G., and D. Chapman. 1996. Tissue flows in grazed plant communities. Pages 3-36 in J. Hodgson and A. W. Illius, editors. *The ecology and management of grazing systems*. CAB International, New York.
- Leriche, H., X. Le Roux, F. Desnoyers, D. Benest, G. Simioni, and L. Abbadie. 2003. Grass response to clipping in an African savanna: Testing the grazing optimization hypothesis. *Ecological Applications* **13**:1346-1354.
- Levine, J. M., P. B. Adler, and S. G. Yelenik. 2004. A meta-analysis of biotic resistance to exotic plant invasions. *Ecology Letters* **7**:975-989.
- Lewis, D., M. J. Singer, R. A. Dahlgren, and K. W. Tate. 2000. Hydrology in a California oak woodland watershed: a 17-year study. *Journal of Hydrology* **240**:106-117.
- Lidicker, W. Z. 1989. Impacts of non-domesticated vertebrates on California grasslands. Pages 135-150 in L. F. Huenneke and H. A. Mooney, editors. *Grassland structure and function: California annual grassland*. Kluwer Academic Publishers, Boston.

- Luo, J., R. W. Tillman, and P. R. Ball. 2000. Nitrogen loss through denitrification in a soil under pasture in New Zealand. *Soil Biology & Biochemistry* **32**:497-509.
- Lusk, W. C., M. B. Jones, P. J. Torell, and C. M. McKell. 1961. Medusahead palatability. *Journal of Range Management* **14**:248-251.
- Major, J., C. M. McKell, and L. J. Berry. 1960. Improvement of medusahead-infested rangeland. Leaflet 123, California Agricultural Experiment Station and Extension Service.
- Malmstrom, C. M., C. J. Stoner, S. Brandenburg, and L. A. Newton. 2006. Virus infection and grazing exert counteracting influences on survivorship of native bunchgrass seedlings competing with invasive exotics. *Journal of Ecology* **94**:264-275.
- Maranon, T., and J. W. Bartolome. 1994. Coast live oak (*Quercus agrifolia*) effects on grassland biomass and diversity. *Madroño* **41**:39-52.
- Maranon, T., and L. V. Garcia. 1997. The relationship between diversity and productivity in plant communities: facts and artefacts. *Journal of Ecology* **85**:95-96.
- Marty, J. T. 2005. Effects of cattle grazing on diversity in ephemeral wetlands. *Conservation Biology* **19**:1626-1632.
- Marty, J. T., S. K. Collinge, and K. J. Rice. 2005. Responses of a remnant California native bunchgrass population to grazing, burning and climatic variation. *Plant Ecology* **181**:101-112.
- McClaran, M., and J. Bartolome. 1985. The importance of oak to ranchers in the California foothill woodland. *Rangelands* **7**:158-161.
- McClaran, M. P., and J. W. Bartolome. 1989. Effect of *Quercus douglasii* (Fagaceae) on herbaceous understory along a rainfall gradient. *Madroño* **36**:141-153.
- McCullough, D. R. 1969. The tule elk: its history, behavior, and ecology. University of California Publications in Zoology, Vol 88. University of California Press, Berkeley.
- McNaughton, S. J. 1979. Grazing as an optimization process - grass ungulate relationships in the Serengeti. *American Naturalist* **113**:691-703.
- Menke, J. W. 1989. Management controls on productivity. Pages 173-200 in L. F. Huenneke and H. A. Mooney, editors. *Grassland structure and function: California annual grassland*. Kluwer Academic Publishers, Boston.
- Menke, J. W. 1992. Grazing and fire management for native perennial grass restoration in California grasslands. *Fremontia* **20**:22-25.
- Merenlender, A. M., K. L. Heise, J. W. Bartolome, and B. Allen-Diaz. 2001. Monitoring shows vegetation change at multiple scales. *California Agriculture* **55**:42-46.

- Meyer, M. D., and P. M. Schiffman. 1999. Fire season and mulch reduction in a California grassland: a comparison of restoration strategies. *Madroño* **46**:25-37.
- Naiman, R. J., and H. Decamps. 1997. The ecology of interfaces: riparian zones. *Annual review of Ecology and Systematics* **28**:621-658.
- Oenema, O., G. L. Velthof, S. Yamulki, and S. C. Jarvis. 1997. Nitrous oxide emissions from grazed grassland. *Soil Use & Management* **13**:288-295.
- Paine, L. K., D. Undersander, and M. D. Casler. 1999. Pasture growth, production, and quality under rotational and continuous grazing management. *Journal of Production Agriculture* **12**:569-577.
- Pietola, L., R. Horn, and M. Yli-Halla. 2005. Effects of trampling by cattle on the hydraulic and mechanical properties of soil. *Soil & Tillage Research* **82**:99-108.
- Pitt, M. D., and H. F. Heady. 1979. The effects of grazing intensity on annual vegetation. *Journal of Range Management* **32**:109-114.
- Ratliff, R. D., D. A. Duncan, and S. E. Westfall. 1991. California oak-woodland overstory species affect herbage understory: management implications. *Journal of Range Management* **44**:306-310.
- Richards, J. H., and M. M. Caldwell. 1985. Soluble carbohydrates, concurrent photosynthesis and efficiency in regrowth following defoliation: a field study with *Agropyron* species. *Journal of Applied Ecology* **22**:907-920.
- Ritchie, M. E., D. Tilman, and J. M. H. Knops. 1998. Herbivore effects on plant and nitrogen dynamics in oak savanna. *Ecology* **79**:165-177.
- Rosiere, R. E. 1987. An evaluation of grazing intensity influences on California annual range. *Journal of Range Management* **40**:160-165.
- Sabater, F., A. Butturini, E. Marti, I. Munoz, A. Romani, J. Wray, and S. Sabater. 2000. Effects of riparian vegetation removal on nutrient retention in a Mediterranean stream. *Journal of the North American Benthological Society* **19**:609-620.
- Safford, H. D., and S. P. Harrison. 2001. Grazing and substrate interact to affect native vs. exotic diversity in roadside grasslands. *Ecological Applications* **11**:1112-1122.
- Sampson, A. W. 1917. Succession as a factor in range management. *Journal of Forestry* **15**:593-596.
- Sampson, A. W. 1952. *Range management principles and practices*. John Wiley and Sons, New York.
- Sampson, A. W., A. Chase, and D. W. Hedrick. 1951. California grasslands and range forage grasses. *University of California Agricultural Experiment Station Bulletin* **724**:2-131.

- Savelle, G. D. 1977. Comparative structure and function in a California annual and native bunchgrass community. PhD. University of California, Berkeley.
- Savelle, G. D., and H. F. Heady. 1970. Mediterranean annual species: their response to defoliation. Pages 548-560 *in* Proceedings of the XI International Grassland Congress.
- Schimel, J. P., L. E. Jackson, and M. K. Firestone. 1989. Spatial and temporal effects of plant-microbial competition for inorganic nitrogen in a California annual grassland. *Soil Biology and Biochemistry* **21**:1059-1066.
- Schlesinger, W. H., and A. M. Pilmanis. 1998. Plant-soil interactions in deserts. *Biogeochemistry* **42**:169-187.
- Shaw, M. R., E. S. Zavaleta, N. R. Chiariello, E. E. Cleland, H. A. Mooney, and C. B. Field. 2002. Grassland responses to global environmental changes suppressed by elevated CO₂. *Science* **298**:1987-1990.
- Singer, F. J., and K. A. Schoenecker. 2003. Do ungulates accelerate or decelerate nitrogen cycling? *Forest Ecology and Management* **181**:189-204.
- Standiford, R. B., and P. Tinnin. 1996. Guidelines for managing California's hardwood rangelands. University of California, Division of Agriculture and Natural Resources Publication 3368.
- Stephens, S. L., and L. W. Ruth. 2005. Federal forest fire policy in the United States. *Ecological Applications* **15**:532-542.
- Stromberg, C. A. E. 2002. The origin and spread of grass-dominated ecosystems in the late Tertiary of North America: preliminary results concerning the evolution of hypsodonty. *Palaeogeography Palaeoclimatology Palaeoecology* **177**:59-75.
- Stromberg, M. R., and J. R. Griffin. 1996. Long-term patterns in coastal California grasslands in relation to cultivation, gophers, and grazing. *Ecological Applications* **6**:1189-1211.
- Talbot, M. W., H. H. Biswell, and A. L. Hormay. 1939. Fluctuations in the annual vegetation of California. *Ecology* **20**:394-402.
- Tate, K. W., E. R. Atwill, N. K. McDougald, and M. R. George. 2003. Spatial and temporal patterns of cattle feces deposition on rangeland. *Journal of Range Management* **56**:432-438.
- Tate, K. W., E. R. Atwill, N. K. McDougald, M. R. George, and D. Witt. 2000. A method for estimating cattle fecal loading on rangeland watersheds. *Journal of Range Management* **53**:506-510.
- Tate, K. W., R. A. Dahlgren, M. J. Singer, B. Allen-Diaz, and E. R. Atwill. 1999. On California rangeland watersheds: timing, frequency of sampling affect accuracy of water quality monitoring. *California Agriculture* **53**:44-48.

- Tate, K. W., D. M. Dudley, N. K. McDougald, and M. R. George. 2004. Effect of canopy and grazing on soil bulk density. *Journal of Range Management* **57**:411-417.
- Thomsen, C. D., W. A. Williams, M. Vayssières, F. L. Bell, and M. R. George. 1993. Controlled grazing on annual grassland decreases yellow starthistle. *California Agriculture* **47**:36-40.
- Turner, C. L., T. R. Seastedt, and M. I. Dyer. 1993. Maximization of aboveground grassland production-the role of defoliation frequency, intensity, and history. *Ecological Applications* **3**:175-186.
- USDA-NASS. 2006. *in*.
- Westoby, M., B. H. Walker, and I. Noy-Meir. 1989. Opportunistic management for rangelands not at equilibrium. *Journal of Range Management* **42**:266-274.
- White, K. L. 1967. Native bunchgrass (*Stipa pulchra*) on Hasting Reservation, California. *Ecology* **48**:949-955.
- Wiens, J. A. 1984. On understanding a non-equilibrium world: myth and reality in community patterns and processes. Pages 439-457 *in* D. R. Strong, D. Simberloff, K. G. Abele, and A. B. Thistle, editors. *Ecological communities: conceptual issues and the evidence*. Princeton University Press, Princeton.
- Williamson, S. C., J. K. Detling, J. L. Dodd, and M. I. Dyer. 1989. Experimental evaluation of the grazing optimization hypothesis. *Journal of Range Management* **42**:149-152.
- Woodmansee, R. G. 1978. Additions and losses of nitrogen in grassland ecosystems. *Bioscience* **28**:448-453.
- Woodmansee, R. G., and D. A. Duncan. 1980. Nitrogen and phosphorus dynamics and budgets in annual grasslands. *Ecology* **61**:893-904.
- Woodward, F. I., M. R. Lomas, and C. K. Kelly. 2004. Global climate and the distribution of plant biomes. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* **359**:1465-1476.
- Xiong, S., and C. Nilsson. 1997. Dynamics of leaf litter accumulation and its effects on riparian vegetation: A review. *Botanical Review* **63**:240-264.
- Xiong, S., and C. Nilsson. 1999. The effects of plant litter on vegetation: A meta-analysis. *Journal of Ecology* **87**:984-994.
- Yoakum, J. D., and B. W. O'Gara. 2000. Pronghorn. Pages 559-577 *in* S. Demaris and P. Karusman, editors. *Ecology and management of large mammals in North America*. Prentice-Hall, Upper Saddle River, NJ.
- Young, J. A. 1992. Ecology and management of medusahead (*Taeniatherum caput-medusae* ssp. *asperum* [Simk.] Melderis). *Great Basin Naturalist* **52**:245-252.

Figure captions

Figure 1. Typical herbaceous production for California annual grassland. The magnitude of response varies positively with rainfall. Grazing has some influence on live biomass at peak standing crop (PSC) by altering the amount of dead biomass or residual dry matter (RDM) at autumn germination (see Fig. 2).

Figure 2. Herbaceous production response to residual dry matter manipulations at 9 sites along a N-S rainfall gradient (modified from Bartolome et al. 1980).

Figure 3. Means by year of DCA site scores (an index of plant community composition), which were normalized to 1992 pretreatment values for headwater springs and their resultant creeks. Mixed effects ANOVA showed DCA site scores were significantly different amongst all 3 grazing treatments at creeks, but not springs indicating alternative, relatively stable equilibria at the former and nonequilibrium at the latter.