

Herbaceous Responses to Livestock Grazing in Californian Oak Woodlands: A Review for Habitat Improvement and Conservation Potential¹

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Abstract

Livestock grazing effects on herbaceous vegetation diversity and ecosystem function are summarized from peer-reviewed literature. Ecosystem responses are linked to grazing management via residual dry matter (RDM), which is alternatively called *litter* or *mulch*. Residual dry matter is the dead herbaceous aboveground biomass remaining on a site at the time of autumn germination in annual grassland and oak woodlands. RDM is known to play an important role in nutrient cycling, soil erosion prevention, and herbaceous species production and composition the following year. Minimum RDM guidelines are used to ensure forage sustainability and protect ecosystem resources. Recent work has indicated that *maximum* RDM standards may be necessary to meet wildlife habitat requirements at both site (for example, burrowing owls) and landscape (for example, kit fox) scales and may be useful for fire-fuels management. Livestock grazing can be a useful conservation tool because managers can control the type, abundance, and spatial and temporal distribution of grazers to meet desired goals. Furthermore, political and economic considerations are rendering prescribed fire, hand mowing, and large native herbivore reintroduction increasingly difficult tools to apply. We review herbaceous vegetation responses to grazing management so that they might be translated to advantages and disadvantages for specific ecosystem and habitat conservation goals on a case-by-case basis.

Key words: annual grassland, biodiversity, conservation, grazing, habitat improvement, livestock, oak woodlands

Introduction

Oak woodlands and savannas occupy 3 million ha in California (Bolsinger 1988, Griffin 1977). Seven series and 57 subspecies have been described within the oak community type (Allen and others 1991). Oak types occupy 52 of California's 58 counties and are widely distributed west of the Sierra Nevada (*fig. 1*). Oak savannas and woodlands generally occur from 60 to 700 masl (meters above sea level), between annual grassland at lower elevations and mixed conifer forests at higher elevations (Barbour and Major 1988). The climate is Mediterranean, with

¹ An abbreviated version of this paper was presented at Planning for Biodiversity: Bringing Research and Management Together, a Symposium for the California South Coast Ecoregion, February 29-March 2, 2000, California State Polytechnic University, Pomona, CA.

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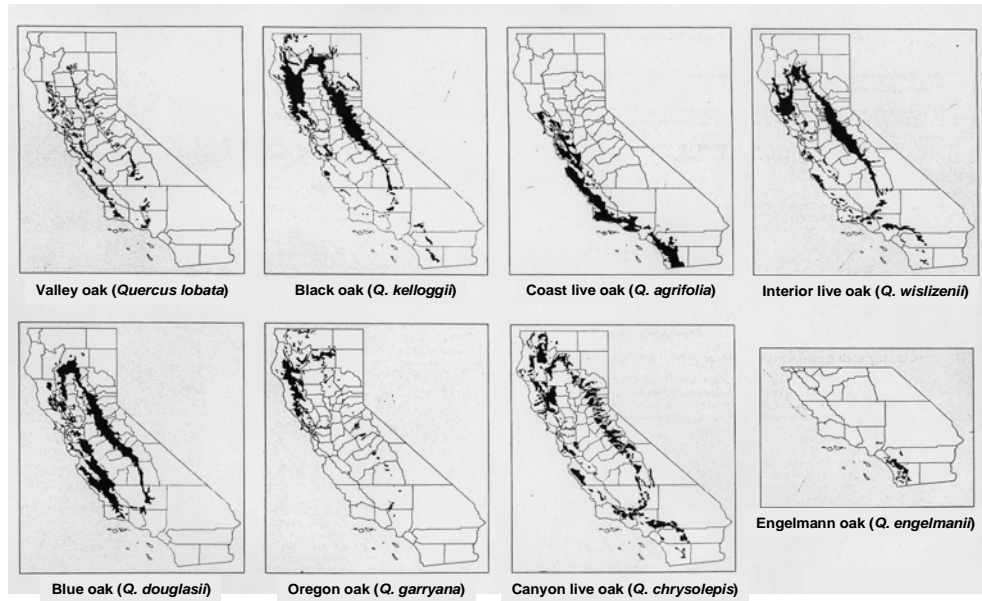


Figure 1—Distribution of eight native oak trees in California (modified from Pavlik and others 1991).

precipitation occurring primarily as rain between October and May. Summer drought results in 3 to 5 months of water deficit (Major 1977).

Dominant trees in the oak woodland include blue oak (*Quercus douglasii*), valley oak (*Q. lobata*), interior live oak (*Q. wislizenii*), coast live oak (*Q. agrifolia*), Oregon white oak (*Q. garryana*), and Engelmann oak (*Q. engelmannii*). These species occur in monospecific to mixed stands (Allen-Diaz and others 1999). Ninety percent of California's oak woodlands are privately owned (Ewing and others 1988). Over 300 species of vertebrates live in oak habitats, including ~80 mammals, 160 birds, 25 amphibians, and 40 reptiles (Standiford and Tinnin 1996). Livestock grazing is the primary agricultural use of oak woodlands, but other economic products include firewood, wildlife, water, and recreation (McClaran and Bartolome 1985, Standiford and Tinnin 1996).

Annual grassland is the major oak understory vegetation, although shrubs and perennial grasses may be an important component in some areas. Native perennial grasses are scattered throughout California (Bartolome and Gemmill 1981, Beetle 1947) and found interspersed within a matrix of annual grasses, forbs, and legumes that are mostly native to the Mediterranean region (Jackson 1985).

Here we review the scientific basis for livestock grazing management on the herbaceous component of California's oak woodlands. The status of this ecosystem over the last 25 years has been addressed in a series of symposia (Pillsbury and others 1997, Plumb 1979, Plumb and Pillsbury 1986, Standiford 1990, Standiford and others 2002), the proceedings of which contain numerous studies of grazing and other management effects on the regeneration of oaks, in addition to many other topics. We do not attempt to review or duplicate this literature. Instead, we emphasize the herbaceous plant communities of oak woodlands and their responses to management so that they might be translated to advantages and disadvantages for specific ecosystem and habitat conservation goals on a case-by-case basis. As much as possible we rely on literature specific to oak woodlands, but with their annual

grassland understory, some references to open grasslands are applicable and cited. Finally, we discuss two approaches for managing and understanding complex systems—Residual Dry Matter guidelines and State-Transition models—that have gained wide use in the field of rangeland resource science as rational approaches to ecosystem management.

Pre-European-settlement Herbaceous Flora

Dominant herbaceous vegetation in California prior to European contact is unknown. Many believe native perennial grasses, particularly the bunchgrass *Nassella pulchra*, once enjoyed a more widespread distribution (Clements 1934, Heady 1977). Hamilton (1998) has argued rather convincingly against overuse of this paradigm, citing over-extrapolation of Clements's climax community concept and the dogma that has derived from it. He suggested that native annuals were once dominant, especially in drier parts of the grassland. Holstein (2001) suggested the rhizomatous perennial grass *Leymus triticoides* dominated the pre-agricultural Central Valley floor. However, his analysis relied on the relict method for which he and others criticize Clements, along with observational accounts of European explorers and settlers.

We know of only two studies providing physical evidence of pre-European settlement composition. Bartolome and others (1986) found greater abundance of distinctive opal phytoliths, silica bodies that are resistant to decay with shapes specific to certain taxonomic groups, at soil depths corresponding to greater than 150 years past. The shapes these phytoliths took were specific to those found in perennial grasses, indicating their greater abundance in the past at that particular site (Jepson Prairie).

The second paper offering some physical evidence of pre-European flora is Mensing and Byrne (1998). They examined preserved pollen in sediment cores from the Santa Barbara channel and determined that the presence of the exotic annual *Erodium cicutarium*—now ubiquitous in much of California—pre-dated European settlement and livestock introduction. They show patterns suggesting it invaded from Baja California prior to the Mission Period in California's history.

Controls on Herbaceous Community Structure

Factors at many spatial and temporal scales interact to control herbaceous productivity in California's annual grasslands, although these factors may be modulated by the presence of oak canopy. In annual grasslands, peak standing crop (aboveground biomass at late spring seed set) varies interannually as a function of the timing and amount of precipitation, temperature (Bentley and Talbot 1948, George and others 1988, Heady 1958, Talbot and others 1939), and edaphic and topographic characteristics (Jackson and others 1990). A typical yearly production curve for the annual grassland understory (*fig. 2*) includes the onset of autumn germination with the first rains over 2.5 cm occurring within a 1-week period. Slow winter growth progresses as temperatures decline, followed by rapid spring growth as soil temperatures increase concurrent with adequate soil moisture. 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 and others 1988).

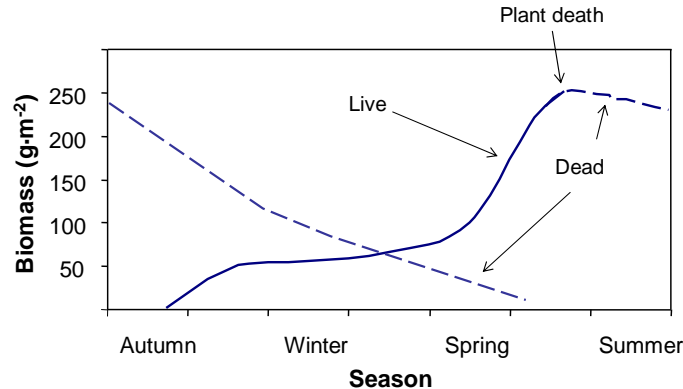


Figure 2—Typical herbaceous production for the University of California’s Sierra Foothill Research & Extension Center (SFREC), a blue oak woodland site NE of Sacramento.

Herbaceous understory production is primarily controlled by interannual weather variability (Connor and Willoughby 1997, Frost and others 1991); however, several workers have demonstrated that tree canopy cover exerts a proximate but variable influence on peak standing biomass depending on regional location, tree density, and tree type (Bartolome and others 1994, Frost and McDougald 1989, Ratliff and others 1991). Relative to open grasslands, canopy cover inhibits herbaceous production in areas of California receiving >50 cm annual precipitation (McClaran and Bartolome 1989), suggesting light reduction as a mechanism. The inverse relationship generally holds for drier portions of the state, where canopy cover serves to attenuate drought stress. From a livestock production perspective, Frost and others (1997) found that an increase in tissue and litter quality per unit biomass under oak canopy in drier regions more than compensated for reduced herbage mass. Nutrient concentrations differed as a result of species composition differences rather than some change in individual plant nutrient use efficiencies.

Species composition differences between oak understory and open grassland have been demonstrated by several authors (Borchert and others 1991, Jackson and others 1990, Marañón and Bartolome 1993, Saenz and Sawyer 1986). Some species appear to be strongly controlled by this dichotomy, but generalizations for California’s oak woodlands are tenuous. A given species may be strongly associated with canopy cover at one site but with open grassland at another. For instance, *Nassella pulchra* is thought to be an open grassland species, but we have observed it scattered under relatively high oak canopy cover in the Sierran foothills (B. Allen-Diaz, unpublished data). Alternatively, *Cynosurus echinatus* is rare in open grassland but common beneath oak canopy throughout the state. Rice and Nagy (2000) sought the mechanism for the spatial separation of *Bromus diandrus* (found under canopy) and *Bromus hordeaceus* (found in the open), showing that interspecific competition was important in the high resource oak canopy soils, but only *B. hordeaceus* could tolerate the harsher conditions of open grassland; there was little evidence of competition between these species in the open. Working in blue oak woodlands of the Sierran foothills, Shlisky (2001) found that aspect, measured at the 10- to 100-m² scale, was a more important determinant of species composition than canopy cover.

Hence, species composition in the herbaceous understory is a complicated mix of time, site, abiotic, and biotic interactions; generalizations are tenuous.

Plant species diversity (measured as species richness) was shown to be highest at intermediate herbaceous biomass levels (Heady and others 1992, Marañón and Bartolome 1994) following the model of Grime (1979) and discussed by Marañón and Garcia (1997) and Garcia and others (1993). Marañón and Bartolome (1994) listed optimum biomass levels for maximum species diversity on California annual grassland/oak woodlands at 35 to 57 g m⁻². They also showed that maintaining an oak overstory component provides for maximal landscape diversity owing to different plant assemblages in canopy and the open.

Grazing Effects on Herbaceous Vegetation

Grazing animals have been part of California grassland, savanna, and woodland ecosystems for thousands of years (Edwards 1992). Before European contact and the establishment of widespread cattle and sheep grazing (Burcham 1957), large herds of pronghorn antelope, tule elk, mule deer, and rodents grazed California grasslands, savannas, and wetlands (Edwards 1996). Many grassland species have evolved habits (for example, prostrate growth) and structures (for example, basal meristems) to avoid or tolerate aboveground tissue loss (Briske 1991).

Grazing animals may influence plant composition and community structure both directly via physical means and indirectly via biogeochemical and biotic feedbacks. McBride and Heady (1968), for example, found that trampling by cattle prevented the encroachment of native coyote bush (*Baccharis pilularis*) into the grasslands of the Berkeley hills. Some evidence exists that high grazing levels promote invasion of undesirable plant species via biological feedbacks (D'Antonio and others 1999); that is, grazers alter the competitive balance of natural communities by interrupting nutrient cycles, altering soil organic matter quality, and creating gaps for colonization, in effect creating an alternate ecosystem more conducive to the invader. However, this model assumes equilibrium-type conditions where biotic interactions play a significant role in shaping the plant community (Wiens 1984). California's Mediterranean climate, with its high interannual rainfall variability, does not lend itself to equilibrium conditions where competitive interactions among plants are allowed sufficient time to affect community structure. From one year to the next, community structure is primarily determined by abiotic constraints associated with autumn germination (Bartolome 1979, Evans and Young 1989).

Evidence for the well-known Intermediate Disturbance Hypothesis (IDH) (Connell 1978, Sousa 1979) is inferred from Marañón and Bartolome (1994) and Bartolome and others (1980), who showed diversity maximized at intermediate levels of aboveground biomass. If intermediate levels of grazing disturbance leave intermediate levels of biomass, these results should apply. However, these results were from coast live oak (non-deciduous) woodlands on the Coast Range (Marañón and Bartolome 1994) and from various open grassland sites (Bartolome and others 1980). The scientific basis for IDH as a mechanism in deciduous blue oak woodlands is lacking. 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 (thereby disturbing vegetation) in areas where livestock were excluded, that is, high cover sites. Hence, any response of diversity to livestock grazing regime changes may be cancelled by rodent activity.

Similar results were noted by Dyer and Rice (1997). Keeley (2002) found slightly reduced herbaceous species richness in livestock-excluded areas compared to grazed areas of blue oak woodlands of the southern Sierran foothills. Nonetheless, these zones maintained greater plant diversity than adjacent mixed-conifer zones at higher elevations irrespective of grazing management, but the oak woodlands were more highly invaded.

Spring-fed wetlands and riparian areas are often the only sources of water in oak woodlands 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 has shown that by years 7 through 10, moderate grazing reduced herbaceous cover, light grazing had minimal effect, and grazing removal significantly increased cover (Jackson 2002). These increases in cover resulted in an undesirable accumulation of plant litter that suppressed subsequent plant productivity. Studies examining grazing effects on vegetation structure in riparian systems other than spring-fed wetlands are few. 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 (Belsky and others 1999, Clary 1995, Fleischner 1994, Kauffman and Krueger 1984, Kauffman and others 1983). However, extrapolation of these results to Mediterranean-type regions should be made very cautiously (Gasith and Resh 1999, Larsen and others 1998). Effects of moderate to light grazing on ecosystems of these regions tend to be overwhelmed by larger scale environmental fluctuations (Allen-Diaz and Jackson 2000, Allen-Diaz and others 1998).

Many studies have sought to determine management techniques for enhancing native perennial grasses, namely grazing, burning, and grazing removal. If target perennial grasses are not present on a site, these treatments will not be effective. However, if present on a site, native perennial grasses have been shown to respond favorably to disturbance treatments, but the particular combination of treatments depends on geography and possibly weather patterns. Bartolome and Gemmill (1981) rejected the notion that *N. pulchra* represents relictual dominance and hypothesized that it likely is a disturbance-adapted species that finds refuge in spaces where light is less limiting than belowground resources. Their hypotheses were largely confirmed by experimental findings of Dyer and Rice (1999). Dyer (2002) found that *N. pulchra* seed from grazed and/or burned individuals germinated and survived at higher rates than seed from undisturbed plants. He invoked *maternal provisioning* as the mechanism by which this advantage is conferred.

Working in Coast Range grassland, Bartolome and others (unpublished data) found a positive response of *Nassella* under post-treatment grazing removal, but not during the grazing removal treatment, indicating some residual effect of their seasonal grazing treatments that was magnified by removal of the disturbance. This aligned with Dyer's and Rice's (1997) work in Valley grassland showing that *N. pulchra* abundance increased only when released from diffuse competition with neighboring annual grasses and forbs.

The studies cited above illustrate the importance of rangeland management based upon scientifically produced information that is applicable to appropriate sites and scales (Bartolome 1989). Range managers control grazing animal type, abundance, spatial distribution, and temporal distribution (season of use). Each of

these singular or interacting factors can produce disparate effects on various ecosystems and ecosystem components. Therefore, grazing efficacy should not be assessed as an “either-or” proposition (in the sense used by Belsky and others 1999).

Grazing Effects at the Ecosystem Level

Grazing can affect ecosystem processes as well as ecosystem structure, though this topic has received considerably less attention in oak woodland understory than open annual grasslands. In general, grazing accelerates carbon and nutrient cycling by effectively bypassing the microbial decomposition pathway. Livestock mineralize plant organic material and return it to the soil and atmosphere as feces, urine, and gas much more quickly than microbes. In perennial grasslands of the Midwest, accelerated nutrient cycling is credited for stimulating net primary productivity (Frank and Evans 1997, Frank and McNaughton 1993, Frank and others 1994). However, similar grazing effects on nutrient dynamics in California annual grassland were not evident (Dahlgren and others 1997, Davidson and others 1993). Nitrogen quickly cycles within annual-dominated ecosystems, where plant species possess low nutrient use efficiencies and high litter qualities irrespective of herbivory (Davidson and others 1990, Jackson and others 1989, Schimel and others 1989).

Dahlgren (1997) describes soils beneath oak canopy as “islands of fertility” because of greater carbon, nitrogen, and phosphorous 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, thereby redistributing ecosystem resources. However, this process would constitute a positive feedback that would be unsustainable in the long-term, depressing herbaceous production in the open; this effect is not evident. An untested hypothesis is that herbivores provide a check on this effect by harvesting herbaceous resources from beneath the canopy and redistributing them relatively more homogeneously across the landscape.

Camping and others (2002) found little effect of grazing on soil chemical properties in blue oak woodland of northern Sierran foothills. Dudley and others (2002), working at the San Joaquin Experimental Range, found higher soil bulk densities in areas with moderate to heavy grazing intensities compared to historically ungrazed areas, indicating deleterious effects on soil physical properties.

Spring-fed wetlands provide many important functions within oak woodland landscapes; livestock grazing modifies these functions. Much of the water exiting oak woodland watersheds passes through these highly productive zones at the terrestrial-aquatic interface (Huang 1997). Wetland vegetation in these zones, typically cattails (*Typha* spp.), sedges, rushes, and perennial grasses, likely acts as a nutrient filter (primarily nitrate) as waters emerge at the soil surface. Jackson (2002) has determined with a paired-plot grazing removal experiment that nitrate concentrations in surface waters where grazing was discontinued for only 2 years were as much as five times greater than grazed counterparts. Furthermore, ungrazed concentrations far exceeded the U.S. Environmental Protection Agency’s maximum standard for surface waters of 714 μm (Fan and others 1987).

that while some species may respond to RDM manipulations in some years, overall plant community composition is relatively insensitive to these changes. Composition seems to be entrained by annual weather patterns producing nonequilibrium conditions that render overall community manipulation via livestock grazing futile. However, this is not to say that a single species such as a native perennial grass or diversity (in the sense of Meyer and Schiffman 1999) cannot be managed for by manipulating the type, intensity, or distribution of grazing (Hatch and others 1999).

Table 1—Minimum residual dry matter guidelines ($g\cdot m^{-2}$) for livestock grazing management in Californian annual grassland.

Precipitation regime (yearly total in cm)	Slope class		
	Lower or flat	Average or gentle	Upper or steep
< 25	22	28	39
25-100	45	67	90
>100	84	112	140

RDM is now the preferred criterion for measuring grazing management effectiveness on California's rangelands. Livestock operators estimate RDM using various methods including harvesting a known area, dry weight rank, and visual estimation (Harris and others 2002). Desired RDM levels are determined based on combinations of slope and average total rainfall (*table 1*). Experiments are currently underway to produce RDM guidelines for oak woodlands where overstory litter complicates the matter. The University of California Cooperative Extension publishes scorecards indicating minimum RDM levels that should sustain system productivity in the face of fluctuating weather conditions. Guidelines like these should be developed for various conservation management objectives.

State-transition Models for Adaptive Management

The emphasis throughout this paper has been on uncertainty and hedged statements about environmental and management effects on grassland understory in oak woodlands. Unraveling of the complexity inherent in this system is occurring, albeit slowly. This is attributable to the plodding pace of the scientific method combined with the context-dependent nature of responses in Mediterranean ecosystems (Gasith and Resh 1999). Experimental information is needed from applied treatment combinations under the range of climate patterns for each setting.

Complex phenomena such as these beg for an organizing framework where results are catalogued and testable hypotheses generated. One such organizing tool, state-transition models, has been espoused for over a decade by rangeland ecologists working in the inherently variable and difficult-to-manage arid and semi-arid regions of Australia and North America (Brown 1994, Filet 1994, Taylor and others 1994, Westoby and others 1989, Whalley 1994). Applications vary, but all state-transition models are simple box-and-arrow diagrams of actual ecosystem states (defined by combinations of vegetation, soils, fauna, and so forth) and transitions among states related to all possible factors—anthropogenic or otherwise (*fig. 4*). Observed and/or hypothetical transitions among states are catalogued, their causes to be tested and

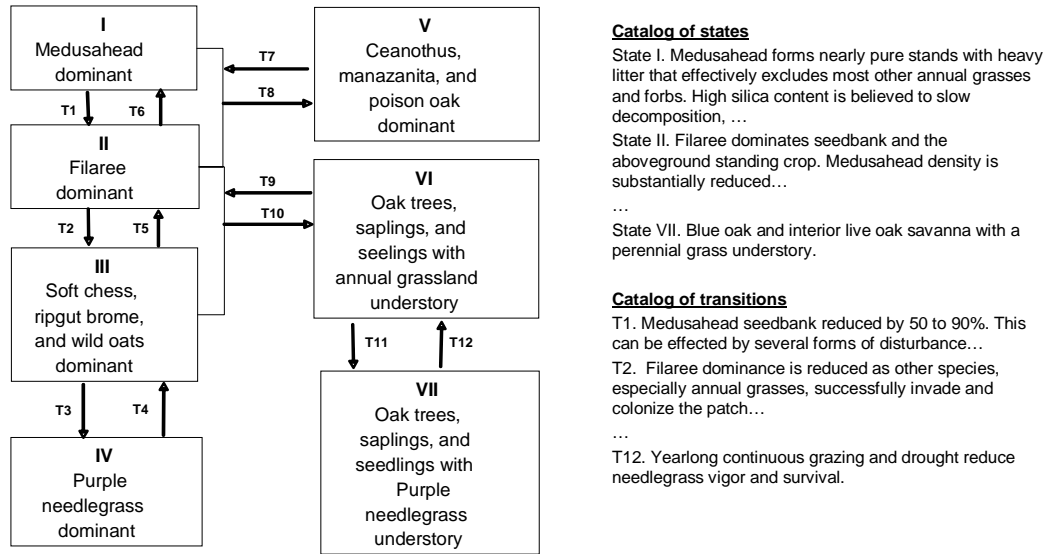


Figure 4—Example of a state-transition model for a Sierran foothill blue oak woodland site. Models such as these could be developed for ecosystem conservation as a means of organizing information and generating testable hypotheses about management induced effects. Note that this model, adapted from George and others 1992, has been simplified; it is shown here only for demonstration of state-transition model structure.

validated or rejected. State-transition models have since been applied to California’s oak woodlands (Huntsinger and Bartolome 1992) and annual grasslands in various forms (George and others 1992, Jackson and Bartolome 2002). However, these applications usually summarize data or hypotheses under relatively restrictive conditions; they seldom allow for filling in gaps in information. More useful models would exhaustively identify as many different weather scenarios and management goals as possible, explicitly differentiating reliable knowledge from hypotheses and conjecture. Publication of this information would minimize redundancy and allow for refinement of research questions.

State-transition models are especially useful where system response is complex and dynamic and therefore should gain wide use in conservation management. They are most useful when data-driven by spatially and temporally explicit results acquired through monitoring and adaptive management.

Livestock Grazing Alternatives

Alternatives to livestock grazing for vegetation management include non-commercial grazing, prescribed fire, herbicidal application, and hand weeding. All are ecologically effective at some scale, yet all possess significant drawbacks. Fire has great potential as a vegetation management tool as it is generally more effective than grazing at removing aboveground biomass. Successful applications include control of yellow starthistle (DiTomaso and others 1999), barbed goatgrass (DiTomaso and others 2001, Hopkinson and others 1999), and medusahead (Murphy and Lusk 1961). However, it is ultimately cost-prohibitive to many managers and agencies because of the high costs associated with maintaining emergency personnel on site during “burn

windows.” Burn events are prone to postponement and cancellation as ideal environmental conditions are sought to maximize the burn’s efficacy while minimizing air pollution. Finally, catastrophe may result from the inevitable escaped prescribed burn.

Potential side effects of herbicide treatment render it a politically as well as an ecologically unsound alternative over extensive areas. Furthermore, long-term efficacy of such treatments tends to be poor (Allen-Diaz and Bartolome 1998). Combinations of herbicidal spraying and livestock grazing are currently being tested for efficacy of yellow starthistle control in northern California. Finally, hand-weeding and non-commercial grazing by waterfowl, goats, and the like for conservation management are effective, politically feasible measures, but at local scales only. Regional, landscape, and even site scales are not manageable by these means.

Future Research

We do not propose livestock grazing as a panacea—a vegetation management tool whose application will help meet every conservation goal. When managed improperly, livestock cause damage to riparian and upland systems and alter habitat, affecting other species. On the other hand, there is a renewed interest in using livestock to achieve specific conservation objectives (Meyer and Schiffman 1999, Pykala 2000, Stolzenburg 2000). This presumes that researchers and managers understand enough about the structure and function of the ecosystem to implement grazing management that will effect the desired response.

Future studies must continue elucidating the relationships between a wide range of grazing intensities and ecosystem responses. Experiments must continue assessing grazing gradients from none to light to moderate to heavy. Furthermore, research should focus on uncovering mechanisms controlling system dynamics in the hope that general principles might evolve. Overgrazing, defined as grazing intensity which will not sustain the desired state of an ecosystem, should not be compared to grazing removal; information from such studies does not advance our understanding but serves to further polarize complex ecological, political, and management issues.

Managing grazing for conservation objectives will require more than the simple RDM scorecards for simultaneously maximizing herbage removal and regrowth used by livestock producers now. Optimal timing and distribution of grazing as well as the type of grazer and grazing intensity will differ for each site and/or species of interest, necessitating monitoring and adaptive management until ecosystem responses under controlled situations can be assessed. Resource consultants are beginning to use remotely sensed RDM estimates in grazing management plans (Standiford and others 1999). Linking geographic information systems to direct management is necessary so that these tools can enjoy wider application. Monitoring efforts should be aimed at multiple spatial and temporal scales for state-transition model development that will lead toward heuristic and even serendipitous knowledge and away from the dogma that surrounds much of rangeland ecology today.

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Management Tools

Residual Dry Matter (RDM) Manipulation

To maintain long-term livestock production, range managers must cope with the vagaries of California climate. While location and yearly weather patterns limit herbaceous productivity in Californian annual grasslands, it has long been known that the amount of mulch remaining at summer's end influences the coming year's peak standing crop (Heady 1956, 1965; Hedrick 1948). Bartolome and others (1980) demonstrated that within a range of residual dry matter (RDM) levels representative of typical grazing intensities, RDM at the time of autumn germination had a positive relationship to peak standing crop of the ensuing year (*fig. 3*). This relationship was roughly consistent along a rainfall gradient from southern San Joaquin Valley to the northern Coast Ranges and has been validated for open grassland at a Sierran foothills site (Aimee Betts, unpublished data). The relationship was weakest at sites with <20 cm total annual rainfall.

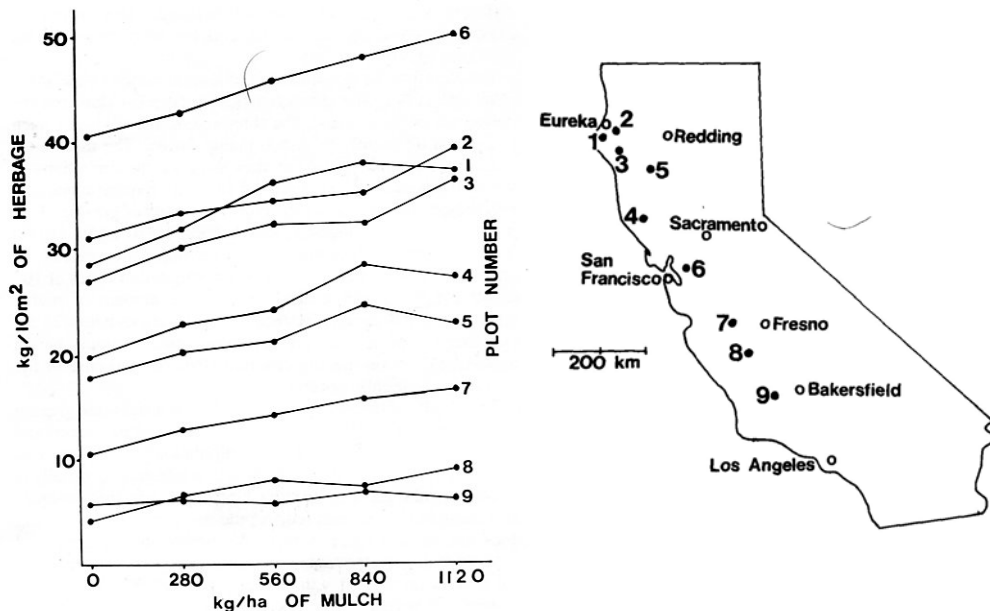


Figure 3—Herbaceous production response to residual dry matter manipulations at nine sites along a N-S rainfall gradient (modified from Bartolome and others 1980).

Mechanisms for this relationship have not been elucidated but are believed to be a favorable combination of light, space, nutrient, and water modifications by moderate levels of RDM. The effects of litter on vegetation in general were reviewed by Xiong and Nilsson (1999). The high RDM extreme, which was not tested by Bartolome and others (1980), probably inhibits production via these same parameters (J.W. Bartolome, unpublished data). Stemming from this work has been an effort to develop minimum RDM guidelines for grazing management in annual grasslands (Bartolome and others 2002, Clawson and others 1982, George and others 1985).

Residual dry matter has been shown to influence species composition on a Mendocino County site (Heady 1965, Pitt and Heady 1978), but recent analysis of the species composition component of the Bartolome and others (1980) data set indicates

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