
Cattle Grazing Impacts on Annual Forbs and Vegetation Composition of Mesic Grasslands in California

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Abstract: *Livestock grazing represents a major human alteration of natural disturbance regimes in grasslands throughout the world, and its impacts on plant communities have been highly debated. We investigated the impact of cattle grazing on the California coastal prairie plant community with a focus on native annual forbs, a number of which are of conservation concern. In spring 2000 and 2001, we surveyed the vegetation community composition, vegetation structure, and soil chemical parameters at 25 paired grazed and ungrazed sites over a 670-km range of the ecosystem. Native annual forb species richness and cover were higher in grazed sites, and this effect was concomitant with decreased vegetation height and litter depth. Soil properties explained less of the variation. Exotic annual grass and forb cover were higher in grazed sites. Native grass cover and species richness did not differ in grazed and ungrazed sites, but cover and species richness of native perennial forbs were higher in ungrazed sites. Our results suggest that cattle grazing may be a valuable management tool with which to conserve native annual forbs in the ecosystem we studied but that grazing differentially affects the various life-history guilds. Therefore, land managers must focus on creating a matrix of disturbance regimes to maintain the suite of species native to these mesic grasslands. The results of this and other studies highlight the importance of considering the adaptation of vegetation communities to disturbance in making recommendations for grazing management.*

Impactos del Pastoreo de Ganado sobre Hierbas Anuales y la Composición Vegetal de Pastizales Mésicos en California

Resumen: *El pastoreo de ganado representa una importante alteración humana de los regímenes de perturbación natural en los pastizales del mundo, y sus impactos sobre las comunidades vegetales han sido ampliamente debatidos. Investigamos el impacto del pastoreo de ganado sobre la comunidad de plantas en la pradera costera de California con énfasis en hierbas nativas anuales, de las cuales varias son de preocupación para la conservación. En la primavera de 2000 y 2001, estudiamos la composición de la comunidad vegetal, estructura de la vegetación y parámetros químicos del suelo en 25 pares de sitios con pastoreo y sin pastoreo en una extensión de 670 km del ecosistema. La riqueza y cobertura de hierbas nativas anuales fueron mayores en sitios pastoreados, y este efecto fue concomitante con una disminución en la altura de la vegetación y la profundidad de la hojarasca. La variación fue menos explicada por las propiedades del suelo. La cobertura de pasto y hierbas exóticas fue mayor en sitios con pastoreo. La cobertura y riqueza de especies de pasto nativo no difirió en sitios con y sin pastoreo pero la cobertura y riqueza de especies de hierbas perennes nativas fue mayor en sitios no perturbados. Nuestros resultados sugieren que el pastoreo de ganado puede ser una valiosa herramienta de gestión para conservar hierbas nativas anuales en el ecosistema que estudiamos pero que el pastoreo afecta diferencialmente a los distintos gremios de historia de vida. Por lo tanto, los gestores de la tierra deben enfocarse en crear una matriz de regímenes de perturbación para mantener al conjunto de especies nativas de estos pastizales méxicos. Los resultados de este y otros estudios resaltan la importancia de considerar la adaptación de comunidades vegetales a la perturbación al hacer recomendaciones de gestión del pastoreo.*

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Introduction

There is increasing concern about the response of species and ecosystems to human-altered disturbance regimes (Foin et al. 1998). For example, extensive research focuses on the negative impacts of disturbances caused by introduced ungulates in grasslands in the western United States (Belsky 1992; Painter & Belsky 1993; Wilcove et al. 1998). In the arid Great Basin and Sonoran deserts, livestock grazing simultaneously results in shrub invasion and a decline in species diversity (Waser & Price 1981; Bahre 1995). Mostly because of the results of research in these arid areas of the western United States, public regulatory agencies and others implicate livestock grazing as a primary cause of the endangerment of many plant species (Czech et al. 1990; Wilcove et al. 1998; U. S. Fish & Wildlife Service 2000).

Despite clear negative effects of grazing in arid systems, data do not confirm similar responses in mesic grasslands. To the contrary, results from research in mesic grasslands suggest the importance of maintaining the types, frequencies, and intensities of disturbance regimes, including grazing, with which species have evolved (Denslow 1980; Collins 1987; Milchunas & Lauenroth 1993; Foin et al. 1998; Knapp et al. 1999).

There are several reasons why grazing may play a more critical role in promoting species richness in mesic than in arid grasslands. Mesic grasslands are more productive than xeric grasslands and thus accumulate higher levels of biomass. This accumulation is particularly acute in grasslands that have been invaded by exotic grasses (D'Antonio & Vitousek 1992). Also, mesic grasslands are prone to shrub and tree invasion, with a consequent loss of grassland species (Foin & Hektner 1986; Hobbs & Mooney 1986; Davis & Sherman 1992; Callaway & Davis 1993). For these reasons, grazing in mesic grasslands may help mitigate the concomitant effects of accumulation of higher levels of biomass, invasion of woody species, and decline of grassland species (Tilman 1993; Foster & Gross 1998; Howe 1999). For instance, the abundance of annual forbs may depend on grazing-mediated physical parameters, such as litter depth (Facelli & Pickett 1991), vegetation height (Foster & Gross 1998), and cover of bare soil (Watt & Gibson 1988; Meyer & Schiffman 1999).

Many previous studies of grazing in grasslands have focused on the effects of grazing on native caespitose grasses ("bunchgrasses"; Coffin & Lauenroth 1996), especially *Nassella pulchra* (Elliott & Wehausen 1974; Bartolome & Gemmill 1981; Heady et al. 1988b; Fossum 1990; Stromberg & Griffin 1996) and *Danthonia californica* (Kotaniemi 1996; Hatch et al. 1999), both of which are thought to have been dominant grass species in California prior to the greatly increased human-induced ecosystem alterations of the last 300 years (Burcham 1975; Bartolome 1986). These species and others appear more resilient to, and possibly even dependent upon,

grazing pressure in the more mesic grasslands (Barry 1972; Bartolome & Gemmill 1981; Heady et al. 1988a), but there has been no systematic survey of their response to grazing.

Because forbs represent the majority of plant species native to grasslands, overlooking this guild could lead to misinterpretation of the effects of grazing on species richness in these communities. Despite this fact, the conservation, restoration, and management of native annual forbs has been largely overlooked, possibly because previous studies have focused on maximizing grassland productivity rather than species diversity (Talbot et al. 1939; Weaver & Rowland 1952; Burcham 1975; Huenneke & Mooney 1989). There have been few studies of the response of native annual forbs to grazing and other disturbances, but grassland-dependent annual forbs are increasingly endangered. Apart from the outright loss of grasslands to agriculture and urban development (Noss et al. 1995), grasslands also face major threats from the introduction of exotic species, changes in disturbance regimes, and habitat fragmentation (Burcham 1975; Foin & Hektner 1986).

Comparisons between adjacent grazed and ungrazed grasslands have been an important tool in determining the effects of grazing (Weaver & Rowland 1952; Fensham et al. 1999; Harrison 1999; Stohlgren et al. 1999; Safford & Harrison 2001). Few researchers, however, have examined these trends across a broad, geographic range and over the majority of the range of a specific vegetation community, a necessity for making conclusive management recommendations. We surveyed paired cattle-grazed and ungrazed sites over a range of 670 km to examine the impact of grazing (and cessation of grazing) on annual forbs native to coastal California grasslands. We focused on native annual forbs because of concern for the increasing rarity of a number of species and because of the paucity of prior documentation of the response of these species to grazing. We hypothesized that species richness and cover of native annual forbs would respond positively to cattle grazing as a result of decreasing vegetation height and litter depth and increasing bare soil area. We also compared the responses of other native and exotic life-history guilds to grazing.

Methods

Study System

Resilience to human impacts of changed disturbance regimes, fragmentation, and exotic species introductions appears relatively high in grasslands along the California coast ("California coastal prairie"), which contain the most intact floral assemblages of any California grassland areas (Heady et al. 1988b) and may contain the highest plant diversity of any North American grasslands

(Stromberg et al. 2002). Coastal prairies are located below 1000 m and within the moderating effects of the ocean (<100 km from the coast). Coastal prairies are patchily distributed from southern Oregon to the Channel Islands of California (Heady et al. 1988b). Characteristic coastal prairie grass species include the perennial *Danthonia californica*, *Deschampsia caespitosa*, *Festuca idahoensis*, and *Festuca rubra*. Coastal prairie hosts approximately 250 forb species, one-third of which are native annuals (Stromberg et al. 2002).

Presently, 25 species of annual forbs native to this ecosystem are in danger of extinction (Tibor 2001). Many of these species are not recovering despite increasing protection on publicly owned land, perhaps because of a lack of appropriate management of natural disturbance regimes (Foin et al. 1998; U.S. Fish and Wildlife Service 2000). Livestock have grazed most grassland in California since the late 1700s, but economic and social pressures have affected the industry in recent decades, so many areas have been subject to less grazing pressure since approximately 1950. Many remaining populations of these species occur primarily in areas grazed by livestock (Fellers & Follette 1990; California Department of Fish & Game 2001).

Site Description

We conducted research in central coastal California from north of Fort Bragg, Mendocino County (lat 39°37'53"N; long 123°47'3"W), to south of Morro Bay, San Luis Obispo County (lat. 35°13'12"N; long 120°52'5"W). This is a 670-km stretch encompassing nearly the full extent of California coastal prairie (Fig. 1). For the years of the survey (2000 and 2001), precipitation averaged 49 cm from the beginning of the rainy season through the end of our survey; it ranged from 33 to 74 cm in 2000 and from 17 to 84 cm in 2001, which is slightly below normal for most of the sites. The increase in variation among sites is likely due to northward and southward extensions of the survey area in 2001. The dry season in this region lasts from May to October and is moderated by frequent fog.

We surveyed 17 paired grazed and ungrazed sites in spring 2000 and 25 paired sites in 2001. Surveys took place between March and June, when species identification and vegetation canopy development were optimal. We began surveys in the south and followed the season northward.

We selected paired sites that met the following criteria: (1) vegetation included plant species typical of coastal prairie (Stromberg et al. 2002); (2) paired plots were separated by <2 km on comparable slopes, soils, and aspects, with no evidence of prior mechanical disturbance; (3) soils were deeper than 40 cm and not ultramafic; (4) slopes were <30%; (5) cattle had been the only domestic animal grazing the grazed sites for at least 10 years; and (6) no domestic animals grazed the ungrazed sites for at

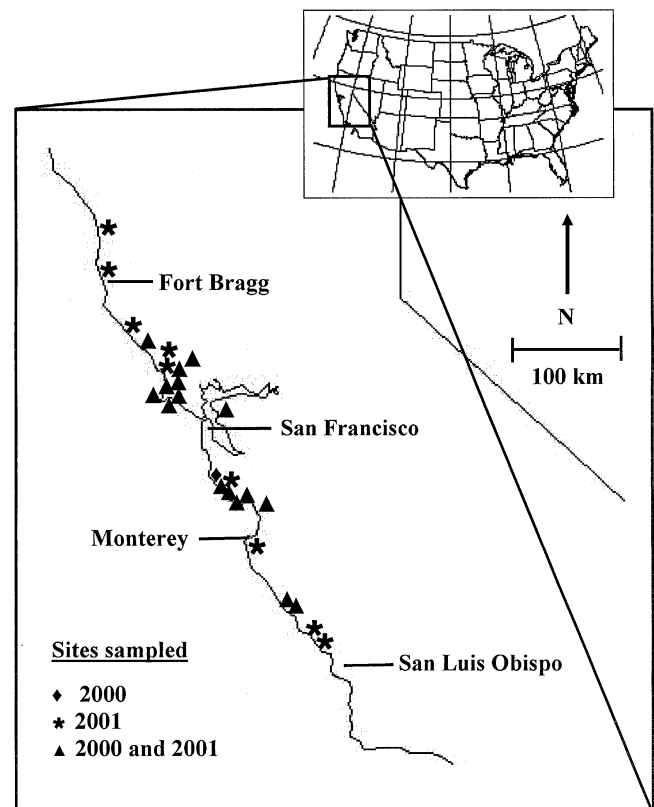


Figure 1. Map of survey sites in eight counties along the California coast.

least 5 years. From this pool of sites, we sampled those for which we could obtain access permission.

Information on grazing regimes was obtained from the landowners. Grazing regimes for the sites varied with respect to duration, stocking rate, and timing. This variation was consistent with our goal of making general conclusions about grazing impact. Most of the grazed areas we used were managed with grazing during the winter growing season only with a variety of grazing regimes.

Community Composition

At each site, we placed five 50-m line transects at least 10 m from the borders of the site. We either randomly located transects where areas of comparable soils and exposures were extensive or systematically located transects where space was limited. In these more limited areas, we spaced the transects equally and as widely apart as possible on comparable soils and exposures. We employed the point-intercept method to quantify the community composition of dominant species. At 1-m intervals, we recorded all species intercepting a 1.8-mm-diameter pin, giving a total of 250 points per site. More than one plant species often intercepted the pin, so the total number of hits was >250. Every 5 m, we recorded litter depth and vegetation height. We sampled litter depth by

pushing a 1.8-mm pin through the litter to the soil surface and measuring the highest horizontal dead-plant material. We quantified vegetation height by lightly dropping a 23-cm-diameter (19-g) plastic disk until it rested on the vegetation and then measured the distance from the center of the disc to the soil surface (Davis 1989; Stewart et al. 2001). To quantify total species richness, we recorded species in a belt transect 1 m wide centered on the line transect if these species had not been recorded along the line transect. We used the Jepson Manual (Hickman 1995) as the reference for nomenclature and source of origin (native vs. exotic) of all species. We deposited specimens of many taxa, including all native annual forbs, at the herbarium of the University of California at Santa Cruz.

Annual Forbs

Because annual forbs (the focus of this study) were patchily and sparsely distributed, we used a different methodology to quantify their species richness and cover. We recorded native annual forbs found in a belt transect 1-m wide centered along each line transect. Allotted survey times were approximately 7 and 22 minutes for grazed and ungrazed belt transects, respectively, following preliminary data on search success for known numbers of short-statured plants in areas of varying vegetation structure (G.F.H. & K.D.H., unpublished data). When we encountered native annual forbs, we recorded aerial cover within the belt transect, litter depth, and vegetation height (as detailed above).

Soil Analysis

During the vegetation survey, we collected a soil sample at each site by mixing 50 cores (2.5 cm in diameter \times 10 cm deep) taken at 5-m intervals along all transects. With standard soil analysis methods (Division of Agriculture & Natural Resources 2002), we analyzed samples for pH, cation-exchange capacity, organic matter, texture, total Kjeldahl nitrogen (TKN), and exchangeable phosphorus, potassium, calcium, and magnesium.

Statistical Analyses

We used paired *t* tests to compare species richness and number of pin intercepts of various life-history guilds recorded along line transects in grazed and ungrazed sites. When we encountered non-normal data, we log-transformed data or arcsine-transformed percentages. If data still did not meet assumptions of normality and homogeneity of variances, we used Wilcoxon two-sample tests on ranked data. Because most species were sparsely distributed, we primarily compared life-history guilds. We also compared cover for a few of the more common species. We categorized species as forbs (all broadleaved monocots or dicots), grasses (monocots in the family

Poaceae), or sedges and rushes (monocots in the families Cyperaceae or Juncaceae).

We performed paired *t* tests to compare native annual forb abundance and diversity in grazed and ungrazed sites. To compare vegetation height and thatch depths in areas with and without native annual forbs, we used data from locations of annual forbs in the belt transect and compared those values with points without native annual forbs along line transects. We used multiple linear regression to analyze the effects of vegetation structure and soil characteristics on the richness and abundance of native annual forbs in all sites. Variables were entered into the model at a value of $p < 0.05$.

Results

Overview

We recorded 261 plant species in 2000 ($n = 17$) and 293 species in 2001 ($n = 25$). (A complete species list is available from G.F.H.). Generally, numbers of species in grazed and ungrazed sites were similar, except that the number of native and exotic annual forb species was higher in grazed sites (native annual forbs: grazed = 29, ungrazed = 18; exotic annual forbs: grazed = 60, ungrazed = 52), and the number of native perennial forb species was higher in ungrazed sites (grazed = 83, ungrazed = 107). None of the soil characteristics differed significantly between grazed and ungrazed sites. Soils were mostly acidic ($\text{pH} = 5.4 \pm 0.5$) sandy loams, low in soil nutrients (TKN = $0.2 \pm 0.1\%$, P = 8.8 ± 6.7 ppm), with low levels of organic matter ($4.3 \pm 1.8\%$) and low cation-exchange capacity (22.7 ± 7.1 meq/100 g). For both years surveyed, grazed sites had lower litter depth and vegetation height and a greater percentage of bare ground than did ungrazed areas (Table 1). Vegetation height and litter depth were highly correlated (Spearman $R^2 = 0.45$ in 2000, $R^2 = 0.77$ in 2001, $p < 0.0001$ in both years).

Native Annual Forb Species Richness and Cover

Species richness and cover of native annual forbs was higher in sites grazed by cattle than in ungrazed sites (Fig. 2). In both grazed and ungrazed sites, native annual forbs represented a small percentage of cover ($<0.1\%$ in both years). Vegetation height and litter depth were lower where native annual forbs were found than where they were not found along the line transect (Table 1). Multiple linear regression of native annual forb species richness on vegetation height, litter depth, and soil characteristics (Ca, TKN, K, Mg, OM, pH) showed that species richness was higher in sites with reduced vegetation height in 2000 ($R^2 = 0.16$, $p = 0.0172$) and in sites with lower Ca and litter depth in 2001 ($R^2 = 0.43$, $p < 0.0001$). Native annual forb cover increased with reduced vegetation height and to a lesser degree with decreasing organic matter in

Table 1. Mean (\pm SE) values for litter depth, vegetation height, and bare ground in grazed and ungrazed survey sites in 2000 ($n = 17$) and 2001 ($n = 25$), and litter depth and vegetation height in areas with and without native annual forbs in 2000 ($n = 672$ with; $n = 1973$ without) and 2001 ($n = 851$ with; $n = 2050$ without).

Variable	Year	Grazed	Ungrazed	p^a	Annual forbs	No annual forbs	p^b
Litter depth (cm)	2000	1.2 \pm 0.1	4.0 \pm 0.2	<0.0001	0.7 \pm 0.0	2.6 \pm 0.2	<0.0001
	2001	1.3 \pm 0.1	5.5 \pm 0.1	<0.0001	1.9 \pm 0.1	3.5 \pm 0.1	<0.0001
Vegetation height (cm)	2000	15.2 \pm 0.3	25.2 \pm 0.5	<0.0001	14.0 \pm 0.5	20.1 \pm 0.8	<0.0001
	2001	13.7 \pm 0.2	27.5 \pm 0.6	<0.0001	14.4 \pm 0.4	21.0 \pm 0.4	<0.0001
Bare ground (%)	2000	4.0 \pm 0.9	1.6 \pm 0.3	0.0076			
	2001	2.6 \pm 0.4	1.5 \pm 0.4	0.0368			

^a Values from grazed and ungrazed sites were compared using paired t tests.

^b Values from sites with and without native annual forbs were compared using unpaired t tests.

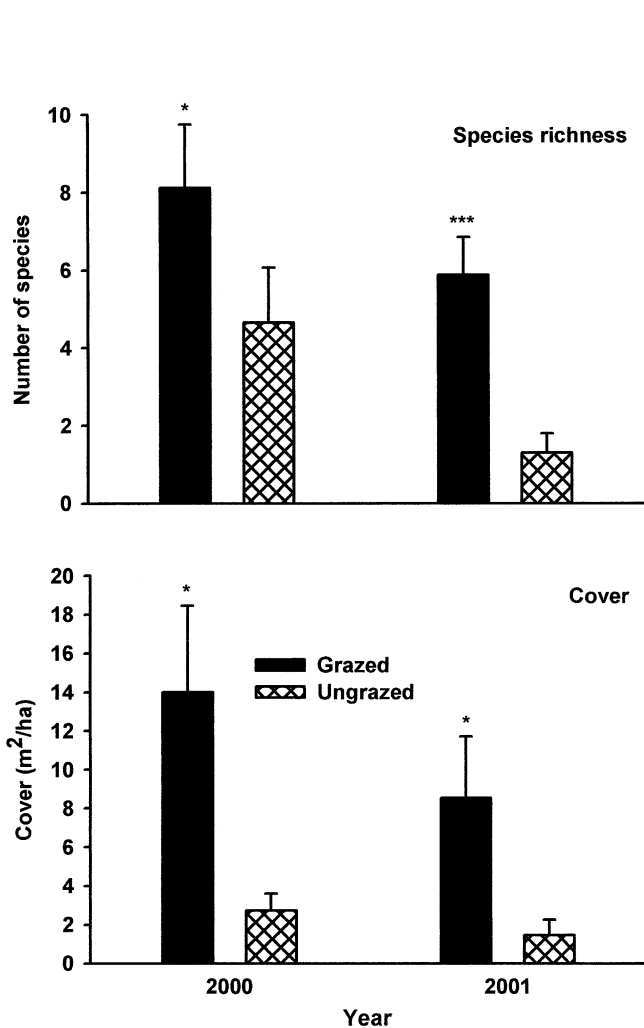


Figure 2. Species richness and cover of native annual forbs in grazed and ungrazed sites in 2000 ($n = 17$) and 2001 ($n = 25$). Error bars indicate 1 SE. Paired t test used: * $p < 0.05$, *** $p < 0.001$.

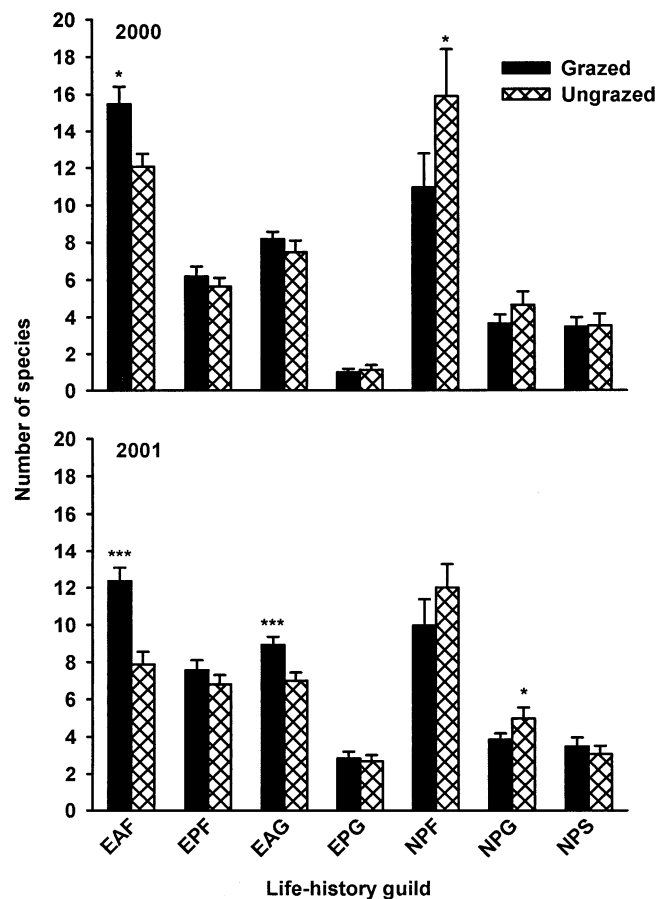


Figure 3. Species richness of common life-history guilds in grazed and ungrazed sites in 2000 ($n = 17$) and 2001 ($n = 25$). Abbreviations: EAF, exotic annual forb; EPF, exotic perennial forb; EAG, exotic annual grass; EPG, exotic perennial grass; NPF, native perennial forb; NPG, native perennial grass; NPS, native perennial sedge or rush. Error bars indicate 1 SE. Paired t test used: * $p < 0.05$, ** $p < 0.01$.

both years (2000: $R^2 = 0.26$, $p = 0.0086$; 2001: $R^2 = 0.38$, $p < 0.0001$).

Plant Community Measurements

The results of most community composition analyses were similar in both survey years; trends in species richness and cover generally paralleled each other (Figs. 3 & 4). Total number of vegetation intercepts was higher in grazed sites in both years (2000: grazed = 478.0 ± 19.1 , ungrazed = 422.8 ± 13.5 ; 2001: grazed = 458.8 ± 11.6 , ungrazed = 399.5 ± 9.3 ; $p < 0.05$ in both years). This is likely a result of the reduced vegetation height, which allows for multiple layers of species. Species richness and cover of exotic annual forbs, like those of native annual forbs, was higher in grazed than in ungrazed sites (Figs. 3 & 4). Both groups were comprised primarily of low-statured plants. Exotic perennial forb cover, but not

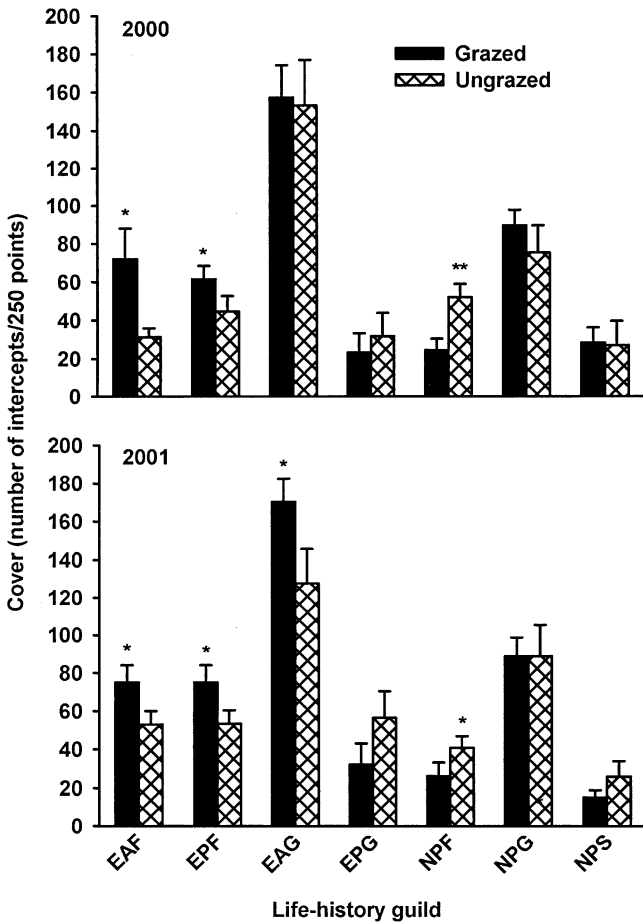


Figure 4. Cover (number of intercepts/250 points) of common life-history guilds in grazed and ungrazed sites in 2000 ($n = 17$) and 2001 ($n = 25$). See Fig. 3 legend for x-axis abbreviations. Error bars indicate 1 SE. Paired t test used: * $p < 0.05$, *** $p < 0.001$.

Table 2. Mean (\pm SE) values compared with t tests for cover (number of intercepts/250 points) of dominant grass species in grazed and ungrazed sites in 2000 ($n = 17$) and 2001 ($n = 25$).

Grass species	Year	Grazed	Ungrazed
<i>Danthonia californica</i>	2000	64.9 ± 8.6^a	31.6 ± 7.6
	2001	40.6 ± 6.2^a	18.5 ± 4.6
<i>Nassella pulchra</i>	2000	6.4 ± 2.6	9.1 ± 3.1
	2001	7.2 ± 2.1	5.6 ± 1.6
<i>Holcus lanatus</i>	2000	10.8 ± 6.3	23.7 ± 11.1
	2001	8.4 ± 3.2	36.5 ± 10.8^b
<i>Bromus</i> spp.	2000	16.5 ± 3.0	22.4 ± 7.5
	2001	21.5 ± 3.7	41.9 ± 11.3
<i>Vulpia</i> spp.	2000	55.6 ± 9.6	62.9 ± 12.7
	2001	48.0 ± 4.5	40.1 ± 7.7

^a $p < 0.0001$.

^b $p < 0.005$.

species richness, was higher in grazed sites. Exotic annual grass species richness and cover were higher in grazed sites in 2001 only, whereas exotic perennial grass cover and richness were similar in grazed and ungrazed sites in both years (Figs. 3 & 4).

Native perennial forbs showed a trend opposite to that of native annual forbs. Native perennial forb cover and species richness were higher in ungrazed sites. Interestingly, neither species richness nor cover of native perennial grasses and native perennial sedges and rushes was affected by grazing, except for slightly higher species richness of native grasses in grazed plots in 2001 (Figs. 3 & 4). The number of native annual grasses and forbs recorded along line transects was sufficiently small to preclude comparisons.

The two dominant native perennial grasses, *Danthonia californica* and *Nassella pulchra*, responded differently to grazing (Table 2). *Danthonia californica* had significantly higher cover in grazed areas during both survey years, whereas the cover of *Nassella pulchra* showed no response. The common exotic perennial grass *Holcus lanatus* had higher cover in ungrazed sites. The cover of both common exotic annual grass genera, *Bromus* and *Vulpia*, showed no response to grazing (Table 2).

Discussion

Native Annual Forbs

Our results with native annual forbs in California coastal prairie suggest that species richness and abundance increase in areas grazed by cattle. This agrees with other research suggesting that species richness responds positively to grazing in similar guilds, including studies of annuals (Grubb 1986; Collins 1987; McNaughton 1993), dicots (Knapp et al. 1999; Bullock et al. 2001), annual dicots (Talbot et al. 1939; Fensham et al. 1999), and other competitively disadvantaged species (Rorison 1971).

Our study, like previous, more localized studies (Talbot et al. 1939; Dunwiddie & Sferra 1991; Davis & Sherman 1992), illustrates the potential negative impacts of cessation of grazing on annual forbs in California coastal prairie. Past researchers have linked the decrease in forbs to increased competition with perennial grasses (Foin & Hektner 1986; Collins 1987; Howe 1999). In our study, cover of both native and exotic perennial grasses, as guilds, was unaffected by grazing. Grazing, however, may have decreased light competition with perennial grasses by reducing their stature.

Our research suggests that vegetation height and litter depth strongly influence the richness and abundance of native annual forb species. Past research also suggests that increased vegetation height and litter depth may limit grassland species richness and abundance (Talbot et al. 1939; Facelli et al. 1988; Weiss 1999), possibly as a result of decreased light levels (Tilman 1993). Litter accumulation is particularly acute in the mostly highly productive California coastal prairie because, with the prolonged dry season, the biomass produced may be slow to decompose (Heady et al. 1988a). Other studies suggest that bare soil is more important than decreasing amounts of litter in increasing species richness and abundance of native annual forbs (Meyer & Schiffman 1999). Although we found more bare soil in grazed sites at the peak of the growing season, the amount of bare soil at the time of seed germination is likely more important.

Whereas this and other research in mesic grasslands suggest that decreased litter depth and vegetation height and increased bare soil favor native annual forbs, these variables may have opposite effects in xeric grasslands. In xeric grasslands, increased plant-litter depth may have favorable effects on annual forbs because it provides shade that may ameliorate the impacts of the harsh microclimate of bare soil areas, increasing plant establishment and growth (Watt & Gibson 1988; Foster & Gross 1998). Correspondingly, research in more xeric grasslands suggests that grazing decreases the cover of annual forbs (Waser & Price 1981; Meyer & Schiffman 1999).

The noted divergence in the responses of xeric versus mesic grassland vegetation to grazing highlights the importance of considering the effects of disturbance regimes in the context of the ecosystem being studied. Varying responses to disturbance may reflect varying evolutionary histories with respect to grazing disturbance (Denslow 1980; Axelrod 1985; Milchunas & Lauenroth 1993). California's fossils record the presence of an extensive Pleistocene megafauna (Edwards 1992) that may have influenced the distribution of grasslands and the evolution of many species. The highly productive mesic grasslands along California's coast have historically sustained an extensive livestock industry. Over evolutionary time, this productivity could have attracted high grazing pressure, which would result in adaptation of plant species to grazing.

Community Composition Response of Grasses and Forbs

Much of the debate regarding grassland grazing has centered around the relative effects of grazing on native and exotic grasses, although the majority of grassland species diversity is not in the grass family. In California, for example, overgrazing has been heralded as facilitating the invasion of exotic grasses (Bartolome 1986), whereas others recommend grazing as a management tool to favor native grasses (Menke 1992). Our results show relatively weak effects of grazing on exotic and native grasses when they are lumped together as guilds. Other studies show positive effects of grazing on exotic grasses in California grasslands (White 1967; Bartolome 1986; Fossum 1990). And research clearly shows that exotic grasses are key to preventing bunchgrass recovery (Bartolome & Gemmill 1981; Foin & Hektner 1986; Brown & Rice 2000; Maron & Jefferies 2001).

The lack of clear trends of grazing effects on grasses in our research is likely due to two factors. First, because of the variation in species across sites, we lumped species into guilds, which may have masked species-specific trends. When examining the native grass *Danthonia californica* separately, we confirmed previous findings that this species responds positively to grazing (Dwire 1984; Heady et al. 1988a; Hatch et al. 1999). Second, our surveys included varied grazing season and intensity, factors that influence community composition (Bukey & Weaver 1939; Fossum 1990; Ash & McIvor 1998).

Our analyses of vegetation community composition suggest much stronger impacts of grazing on forbs than on grasses. As with native annual forbs, exotic annual forbs had higher species richness and cover in grazed sites in both years. Low-statured annual plants may be favored by grazing (Noy-Meir et al. 1989; McIntyre et al. 1995). Most of the native and exotic annual forbs in our survey were low-statured, and, as discussed previously, annuals generally benefit from increased bare ground for recruitment in mesic systems.

Interestingly, exotic perennial forb cover was higher in grazed sites, whereas native perennial forb cover and species richness were higher in ungrazed sites. Most of the exotic perennial forbs we recorded were low-statured species common in disturbed areas. The native perennial forbs generally fell into one of two categories: tall-statured plants that do not reproduce when clipped or slower-growing species that primarily reproduce vegetatively. In contrast, others have found that native perennial forbs, especially low-statured species, respond negatively to increased plant litter and canopy height (Foster & Gross 1998; Maron & Jefferies 2001).

Management Recommendations

Research on the effect of grazing across the majority of the range of an ecosystem type is critical to making broad

management recommendations. Studies at localized sites are important to tease out site-specific differences, which our results mask, but results are often misleading when they are generalized beyond their geographic sample extent (Hurlbert 1984).

Our research highlights the importance of considering the adaptation of the ecosystem to grazing disturbance rather than categorizing grazing as good or bad from a conservation standpoint. As discussed previously, evolutionary history and amount of precipitation are among the important factors determining an ecosystem's response to grazing.

Our research strongly demonstrates that a disturbance such as grazing may have positive and negative aspects on conservation of different native guilds and even different species within each guild. We originally sought to test the anecdotal observation that grazing was an important strategy for maintaining and increasing populations of a number of native annual forb species of concern. Our results support this hypothesis but also show that grazing has negative effects on native perennial forbs, which comprise a larger number of species in these grasslands. Unfortunately, this makes management for a full suite of native species more complicated. Conservation of the native California coastal prairie vegetation community requires a matrix of grazed and ungrazed grasslands in space and time. Because many of the remaining coastal grasslands are small parcels, land managers will need to cooperate on a landscape level to maintain such a mosaic.

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