



Community-level consequences of cattle grazing for an invaded grassland: variable responses of native and exotic vegetation

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Biological invasions; Coastal grasslands; Community responses to grazing; Exotic plants; Geographic origin; Herbivory; Life-form and life-history characteristics

Nomenclature

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Abstract

Questions: Does grazing by cattle mediate the composition of a coastal grassland community and do native and exotic taxa from different plant groups, based on life-history and life-form characteristics, vary in their response to grazing? To what degree does grazing impact the growth and fecundity of *Bromus diandrus*, the most dominant exotic grass invader in this system?

Location: Coastal grassland/prairie near Carmel, central California, USA.

Methods: Using a 3-yr enclosure experiment, we evaluated the effects of light winter/spring grazing by cattle (average of 0.75 cow-calf pairs-ha⁻¹) on species richness and percentage cover of native and exotic plants from different life-history and life-form groups.

Results: We found that cattle grazing reduced total vegetative cover by 25% and increased bare ground by 40%. Grazing also caused a 70% reduction in above-ground plant biomass and a 40% reduction in the cover of exotic annual grasses, which were by far the most dominant group in this system. Grazing also reduced the height and spikelet production of the exotic annual grass *B. diandrus*. In contrast, grazing increased the cover of exotic annual forbs by 15%. Contrary to our expectations, grazing did not affect the cover of native forbs and grasses, and we hypothesize that these taxa possess life-history characteristics and/or depleted seed banks that prevented them from responding to grazing during our experiment. Grazing also did not affect the species richness of any native or exotic plant group.

Conclusions: Our 3-yr enclosure experiment has shown that grazing by cattle caused major changes in a coastal grassland community, with the responses of native and exotic taxa having different life-history and life-form characteristics varying markedly. Understanding the responses of these divergent groups is not only important for basic research evaluating the effects of mammalian herbivores on plant communities, but is also critical for developing science-based approaches for sustainably managing invaded grasslands.

Introduction

Native, exotic (i.e. feral) and domesticated ungulates are important herbivores in many terrestrial regions of the world and commonly influence the structure and dynamics of plant communities and ecosystems (McNaughton et al. 1989; Huntly 1991; Collins et al. 1998; Olf & Ritchie 1998; Knapp et al. 1999; Díaz et al. 2007; Nunez et al.

2010). Because of the global nature of biological invasions, these herbivores increasingly inhabit landscapes that are dominated by invasive exotic plant species, and such invaders exert strong influences on resident communities by altering competitive dynamics (Levine et al. 2003), fire regimes and nutrient cycling (D'Antonio & Vitousek 1992; Dukes & Mooney 2004; D'Antonio & Hobbie 2005). How ungulate herbivores impact these invaded landscapes and

alter the competitive dynamics among resident plant taxa is of great interest to ecologists and conservation biologists alike, and is likely to vary considerably depending on a range of factors, including the ecological characteristics of resident plant taxa.

Plant species from different groups based on life-history and life-form characteristics may vary greatly in their responses to herbivory, as might native and exotic species from within the same group. Such taxa often differ considerably in their responses to disturbance and in their growth, colonization and competitive abilities (Grime 1979; Hobbs & Huenneke 1992; McIntyre et al. 1995; Lavorel et al. 1999; Díaz et al. 2007; van Kleunen et al. 2010; Godoy et al. 2011). For example, a meta-analysis by Parker et al. (2006) showed that a wide range of native herbivores reduced the relative abundance of exotic plants, whereas a similarly diverse group of exotic herbivores increased the relative abundance and species richness of exotic plants. In addition, other studies have found that both native ungulates (Johnson & Cushman 2007) and cattle (Díaz et al. 2007) increased the abundance of annual plants while either having no effect on or decreasing the abundance of perennial species. Herbivores that have large negative effects on plant species in one life-history/life-form group may also influence their competitive interactions with species from other groups. For example, a herbivore-induced decrease in abundance of members from one group may cause an increase in the abundance of taxa from other competitively subordinate groups. To develop a comprehensive understanding of the impacts of ungulate herbivores on vegetation and the utility of grazing as a conservation tool, research must address the responses of native and exotic species from different life-history and life-form groups.

Grasslands in California have a long history with both native and domesticated ungulates (Jackson & Bartolome 2007) and are one of the most invaded systems in the world, having undergone a nearly complete transformation from perennial grass- and forb-dominated native flora (the ratio of grasses to forbs is debated; see Minnich 2008) to assemblages dominated by exotic annual grasses (Seabloom et al. 2006; D'Antonio et al. 2007). Numerous factors have contributed to this dramatic transformation, including historical droughts, intensive agriculture and livestock grazing (Heady 1988; Heady et al. 1988, 1992; Holstein 2001; Corbin & D'Antonio 2004). The increased dominance of exotic annual grasses has adversely affected native bunchgrasses through increased competition (Dyer & Rice 1997; Brown & Rice 2000) and led to the accumulation of tremendous amounts of above-ground dead biomass that can negatively affect germination, recruitment, species richness and relative dominance of native taxa

(Bergelson 1990; Facelli & Pickett 1991; Tilman 1993; Foster & Gross 1998), and even lead to positive feedbacks that further promote exotic annual grasses (Wolkovich et al. 2009).

Given the extraordinary degree and spatial scale of these invasions, a major challenge is to understand how domesticated herbivores influence the dominance of exotic plants and the native species that remain. Although implicated in the initial demise of native grasslands (see Fleischner 1994), cattle grazing has been shown to reduce the dominance of exotic plant invaders (Hatch et al. 1999; Harrison et al. 2003; Hayes & Holl 2003a; Marty 2005), particularly when the focus is on one or a few target species (Dyer & Rice 1997; Dyer 2003; Bartolome et al. 2004). However, despite growing use of cattle grazing as a conservation and restoration tool, its effects on invaded grasslands are quite variable. For example, studies in California have found that cattle grazing can positively impact the abundance of some native groups (Marty 2005), negatively impact the species richness of native plants (Harrison et al. 2003), or have a mixture of positive and negative effects on abundance of different plant groups in the community (Hayes & Holl 2003a; Bartolome et al. 2004). Possible explanations for these mixed results include variation in the types of grasslands studied (mesic vs. xeric), approaches employed in the study (experimental vs. comparative) and focus of the project (single species or group vs. the entire plant community). For example, only a handful of studies have evaluated the effects of cattle grazing on native and exotic vegetation in an entire grassland community (Harrison et al. 2003; Hayes & Holl 2003a; Kimball & Schiffman 2003; Bartolome et al. 2004). Additional studies have focused on the impact of grazing on a few of the dominant exotic or native species in a grassland community (Hatch et al. 1999) or used simulated herbivory (Hayes & Holl 2003b; Kimball & Schiffman 2003). However, due to the mixed results of these studies, further experimental research is needed to understand the impacts of cattle grazing on plant communities in invaded grasslands.

Here, we summarize results from a 3-yr enclosure experiment designed to evaluate the influence of cattle grazing on the entire plant community in a mesic coastal grassland in central California. The primary goal of our research was to determine how cattle grazing altered the cover and species richness of native and exotic taxa from different plant groups based on life-history and life-form characteristics. Secondly, we addressed the impact of cattle grazing on above-ground plant biomass and the growth and fecundity of *Bromus diandrus*, the most dominant exotic invader in our system. Exploring these issues will aid in the development

of a framework for understanding the responses of plant communities to a dominant introduced herbivore and the effectiveness of grazing as a tool for restoring degraded grasslands.

Study system

This research was conducted in a coastal grassland at Palo Corona Regional Park (PCRP), 1.6 km south of Carmel in Monterey County, California, USA (36°29'07.4" N, 121°53'32.7" W). The 1760-ha regional park is located along the Santa Lucia Range in the Pacific Coast Range and hosts a variety of vegetation types, including coastal grassland, scrub and chaparral, oak woodland, redwood forest and Monterey pine forest. The grassland regions of PCRP are historic ranchlands where grazing began in the late 18th century when the Carmel Mission was established nearby (G. Paddock, pers. comm.). Throughout the following 230 years, private landowners grazed cattle on these grasslands annually until 1999 (T. Jenson, pers. comm.). In 2007, cattle were re-introduced to assess their impacts on the plant community and effectiveness as a conservation tool for managing the grassland.

The study region experiences a mediterranean-type climate consisting of cool, moist winters and warm, dry summers, as well as a strong coastal influence that results in frequent summer fog. The 20-yr average annual rainfall preceding this study was 527 mm, which falls predominantly from November through April. However, annual rainfall during our 3-yr study period ranged from 346 to 410 mm (2007, 346 mm; 2008, 377 mm; 2009, 410 mm; National Climatic Data Center 2009).

Our study sites were located in the Panoche Management Unit of PCRP, a 154-ha parcel 4.8 km inland from the Pacific Ocean. Soils in the area are primarily of the Cieneba (shallow sandy loam, typic xerorthents) and Sheridan (granitic sandy loam, thermic pachic haploxerolls) series (Natural Resources Conservation Service). The Panoche Unit is mainly comprised of ridgelines dominated by grassland species that intergrade with shrubland species on the steeper slopes below the ridgelines. Our study sites were located at the intersection of these two community types, with an average shrub cover of approximately 20%. The shrub species were all native and consisted of *Eriogonum parvifolium*, *E. nudum* and *Lupinus arboreus*. The grassy ridges were dominated by exotic annual grasses (*B. diandrus*, *B. hordeaceus*, *Lolium multiflorum*, *Avena barbata* and *Aira caryophylla*), but also supported low densities of native perennial grasses (*Nassella pulchra*, *Danthonia californica*, *Poa secunda* and *Bromus carinatus*). The two most common forb species were *Hypochaeris glabra*, an exotic

annual, and *Eschscholzia californica*, a native annual (see Table 1).

Methods

Cattle enclosure experiment

To address the impacts of cattle grazing on plant communities, we established a cattle enclosure experiment in January and February of 2007 on the ridge-top grasslands in the Panoche Management Unit of PCRP. This experiment consisted of 20 8 m × 8 m plots distributed across five sites, with each site containing four plots. The location of each site was selectively chosen within regions of grassland accessible to cattle, and where grassland species and shrubs co-occurred. We visually matched plots within sites for similarity in slope, aspect, elevation and vegetation composition. We also grouped plots within sites into two blocks based on proximity, and randomly assigned one plot in each block to receive fencing that excluded cattle and left the other plot unmanipulated to serve as a control (two controls and two enclosures per site). All plots were separated by at least 2 m and had four steel t-posts demarking their corners. Plots that excluded cattle had four additional mid-posts, corner bracing and five strands of barbed wire encircling them.

Starting in 2007, cattle were introduced to our study area during late winter and spring each year of this 3-yr experiment. The site was grazed with 69 cow-calf pairs in 2007 (22 March to 16 April), 63 pairs in 2008 (17 February to 30 March) and 53 pairs and two bulls in 2009 (23 January to 11 April). Each year, cattle were removed from the Panoche Unit when above-ground plant biomass in the spring reached levels necessary to yield autumn residual dry matter (RDM) values of ca. 1350–2000 kg·ha⁻¹ (1200–1800 pounds·acre⁻¹; see Bartolome et al. (2006) for details on how this was achieved). This RDM level approximates light grazing intensity and was established by the land managers of PCRP based on the recommendations of Bartolome et al. (2006) for sustainable grazing in California's coastal grasslands.

Vegetation responses to cattle grazing

After cattle grazing occurred in the spring for each of 3 years, we conducted all sampling at peak biomass, which did not differ between grazed and ungrazed areas. Peak biomass also corresponded to maximal phenological development for most species. We harvested all above-ground plant biomass from two 25 cm × 25 cm quadrats placed in the central region of each plot, away from areas used for vegetation sampling (see below) and in different locations each year. We pooled the two samples from each plot, dried them at 60 °C for 48 h, and weighed them. So that

Table 1. Mean (± 1 SE) percentage cover for plant species averaged across 3 years (2007–2009) as a function of cattle grazing treatment (grazed, ungrazed) and grouped by geographic origin, life history and life form group designations.

Species	Family	Mean % Cover/Plot	
		Grazed	Ungrazed
A. Exotic annual grasses			
<i>Aira caryophylla</i>	Poaceae	1.07 (0.68)	0.78 (0.46)
<i>Avena barbata</i>	Poaceae	1.39 (0.51)	1.75 (0.64)
<i>Bromus diandrus</i>	Poaceae	29.80 (3.47)	51.28 (5.72)
<i>Bromus hordeaceus</i>	Poaceae	8.61 (1.37)	17.20 (3.14)
<i>Hordeum murinum</i>	Poaceae	0.15 (0.15)	0
<i>Lolium multiflorum</i>	Poaceae	6.81 (1.40)	8.57 (2.26)
<i>Vulpia bromoides</i>	Poaceae	0.56 (0.14)	1.98 (1.12)
B. Native perennial grasses			
<i>Bromus carinatus</i>	Poaceae	0.35 (0.35)	0
<i>Danthonia californica</i>	Poaceae	0.02 (0.02)	0
<i>Nassella pulchra</i>	Poaceae	0.39 (0.19)	0.26 (0.26)
C. Exotic Annual Forbs			
<i>Anagallis arvensis</i>	Primulaceae	0.93 (0.47)	0.78 (0.50)
<i>Cerastium glomeratum</i>	Caryophyllaceae	0	0.02 (0.02)
<i>Erodium botrys</i>	Geraniaceae	0.61 (0.59)	0.31 (0.21)
<i>Erodium cicutarium</i>	Geraniaceae	6.61 (1.34)	2.80 (0.48)
<i>Geranium molle</i>	Geraniaceae	0.39 (0.28)	0.80 (0.62)
<i>Hypochaeris glabra</i>	Asteraceae	9.69 (1.88)	4.00 (1.07)
<i>Lactuca</i> sp.	Asteraceae	0.30 (0.26)	0.02 (0.02)
<i>Silene gallica</i>	Caryophyllaceae	2.30 (0.40)	1.02 (0.18)
<i>Sonchus oleraceus</i>	Asteraceae	0	0.04 (0.04)
<i>Sonchus</i> sp.	Asteraceae	0.02 (0.02)	0
<i>Stellaria media</i>	Caryophyllaceae	3.91 (0.99)	2.52 (0.78)
<i>Torilis nodosa</i>	Apiaceae	0.06 (0.04)	0.24 (0.16)
<i>Vicia sativa</i>	Fabaceae	0.07 (0.07)	0.09 (0.09)
D. Native annual forbs			
<i>Agoseris</i> sp.	Asteraceae	0.28 (0.15)	0.04 (0.02)
<i>Calandrinia ciliata</i>	Portulacaceae	0.11 (0.05)	0.13 (0.07)
<i>Clarkia purpurea</i>	Onagraceae	0.30 (0.13)	0.48 (0.35)
<i>Clarkia unguiculata</i>	Onagraceae	0.39 (0.23)	0.78 (0.40)
<i>Crassula conata</i>	Crassulaceae	0.04 (0.02)	0
<i>Cryptantha clevelandii</i>	Boraginaceae	0.02 (0.02)	0.11 (0.07)
<i>Daucus pusillus</i>	Apiaceae	0.44 (0.21)	0.50 (0.27)
<i>Eschscholzia californica</i>	Papaveraceae	4.52 (0.92)	6.52 (1.71)
<i>Galium aparine</i>	Rubiaceae	2.41 (1.20)	0.72 (0.38)
<i>Gilia angelensis</i>	Polemoniaceae	0.52 (0.52)	0.06 (0.06)
<i>Gnaphalium californicum</i>	Asteraceae	0	0.04 (0.04)
<i>Lepidium nitidum</i>	Brassicaceae	0.11 (0.07)	0.07 (0.06)
<i>Linanthus grandiflorus</i>	Polemoniaceae	0	0.06 (0.06)
<i>Lotus purshianus</i>	Fabaceae	0.04 (0.02)	0.02 (0.02)
<i>Lotus strigosus</i>	Fabaceae	0.02 (0.02)	0.04 (0.02)
<i>Lupinus nanus</i>	Fabaceae	0.46 (0.15)	1.20 (0.49)
<i>Madia elegans</i>	Asteraceae	3.35 (1.06)	3.81 (1.10)
<i>Pterostegia drymarioides</i>	Polygonaceae	0.26 (0.26)	0.28 (0.21)
<i>Stephanomeria virgata</i>	Asteraceae	0.24 (0.12)	0.46 (0.23)
<i>Trifolium gracilentum</i>	Fabaceae	0.96 (0.22)	1.35 (0.39)
<i>Trifolium microcephalum</i>	Fabaceae	0.67 (0.27)	0.33 (0.13)
<i>Viola pedunculata</i>	Violaceae	0.06 (0.06)	0.54 (0.30)

Table 1. (Continued).

E. Exotic perennial forbs			
<i>Linum bienne</i>	Linaceae	0.04 (0.04)	0
<i>Rumex acetosella</i>	Polygonaceae	4.02 (0.83)	5.87 (1.37)
<i>Trifolium pratense</i>	Fabaceae	0	0.04 (0.02)
F. Native perennial forbs			
<i>Chlorogalum pomeridianum</i>	Liliaceae	0.02 (0.02)	0.26 (0.15)
<i>Dichelostemma capitatum</i>	Liliaceae	0.07 (0.04)	0.20 (0.10)
<i>Galium trifidum</i>	Rubiaceae	0.17 (0.10)	0.06 (0.04)
<i>Heterotheca sessiliflora</i>	Asteraceae	0.06 (0.06)	0
<i>Phacelia ramosissima</i>	Hydrophyllaceae	0.06 (0.06)	0.33 (0.33)
G. Native Shrubs			
<i>Eriogonum nudum</i>	Polygonaceae	2.76 (1.41)	2.91 (1.02)
<i>Eriogonum parvifolium</i>	Polygonaceae	16.17 (3.91)	13.44 (3.01)
<i>Lotus scoparius</i>	Fabaceae	1.22 (0.29)	2.33 (1.23)
<i>Lupinus arboreus</i>	Fabaceae	0.26 (0.24)	0

our results were comparable to other studies, we converted biomass data from grams 0.125 m^{-2} to grams m^{-2} .

To evaluate the influence of cattle grazing on the entire plant community, we sampled the vegetation inside our 20 8 m \times 8 m plots using standard point-intercept methods (Mueller-Dombois & Ellenberg 1974). At peak biomass in the spring of 2007, 2008 and 2009, we recorded all plant species encountered at 45 points in each of four permanent 1 m \times 1 m quadrats, one established within the centre of each plot quarter (the 45 points were located at intersection points in a 9 \times 5 grid composed of 5 cm \times 10 cm rectangles). We calculated the absolute percentage cover of the various plant groups by dividing the number of occurrences by the total number of sampled points (45 points). Because we regularly encountered multiple plant taxa at a single point, percentage cover values frequently exceeded 100%. To quantify species richness, we also conducted whole-plot searches to record all species present in each plot. For these cover and richness data, we grouped species by geographic origin (native and exotic) and life-history and life-form characteristics to generate seven plant groupings: (1) exotic annual grasses; (2) native perennial grasses; (3) native annual forbs; (4) exotic annual forbs; (5) native perennial forbs; (6) exotic perennial forbs and; (7) native shrubs (native annual grasses, exotic perennial grasses and exotic shrubs did not occur in our enclosure experiment). All nomenclature and origin information follows Hickman (1993). We also calculated absolute percentage cover of total vegetative cover and bare ground.

To evaluate the effects of cattle grazing on the most dominant exotic annual grass in our system, *B. diandrus*, during our community sampling described above, we found the nearest intact individual grass tiller to six standardized

locations within each of the four permanent quadrats in all plots, measured its height and determined the number of spikelets produced (emergent and non-emergent). Unlike some other exotic annual grasses, *B. diandrus* regrew very little after grazing cattle were removed each year (M. J. Skaer & J. H. Cushman, pers. obs.).

Statistical analysis

Unless noted otherwise, we performed all analyses using general linear models (GLMs) in SAS 9.1.3 (SAS Institute, Inc., Cary, NC, USA). All models used grazing treatment (cattle present or absent) as a fixed factor, with site (1–5) and block nested in site as random factors, and year as a repeated measure (2007–2009). For all repeated-measures analyses, we evaluated terms containing year using Pillai's trace, which is the most robust to violations of assumptions (Schiener 2001). We log-transformed data when we encountered non-normal data or unequal variances. We analysed data on above-ground plant biomass ($\text{g}\cdot\text{m}^{-2}$), percentage cover of total vegetation and percentage bare ground using repeated-measures GLMs. We analysed the percentage cover and species richness data using two repeated-measures multivariate analysis of variances (MANOVAs). The first MANOVA used absolute percentage cover of seven plant groupings as response variables (exotic annual grasses, native perennial grasses, native annual forbs, exotic annual forbs, native perennial forbs, exotic perennial forbs and native shrubs), where quadrat data were treated as subsamples. The second MANOVA used species richness of these plant groupings as the response variables. For MANOVAs with significant grazing main effects, we proceeded with separate 'protected' GLMs using each of the seven plant groups as the response variable. This procedure addresses possible correlations among multiple dependent variables (Schiener 2001; Alvarez & Cushman 2002; Cushman et al. 2004).

We analysed data on *B. diandrus* height and fecundity in 2009 using two linear mixed models with Type III estimation. This type of analysis was preferable because *B. diandrus* was missing from some quadrats and the mixed-model approach handles unbalanced designs more appropriately than the GLM that we used elsewhere (Littell et al. 2006).

Results

In our study system, light winter/spring grazing by cattle reduced above-ground plant biomass ($F_{1,9} = 41.44$, $P < 0.0001$), although the effects of grazing varied among years ($F_{2,8} = 6.37$, $P = 0.0221$; Fig. 1), being highest in the third year (2009) of our experiment. Overall biomass production also varied significantly among the 3 years of our

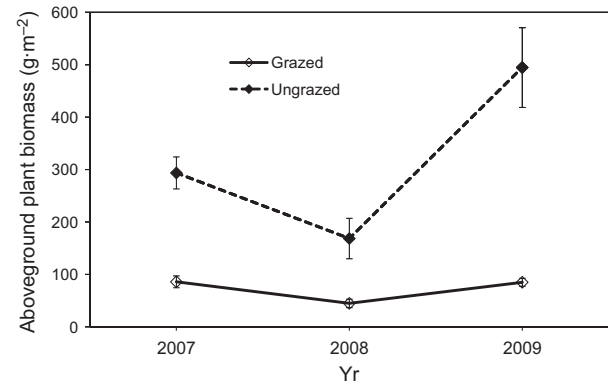


Fig. 1. Mean (± 1 SE) above-ground dry plant biomass ($\text{g}\cdot\text{m}^{-2}$) as a function of cattle treatment (present, absent) and year (2007–2009).

study ($F_{2,8} = 10.78$, $P = 0.0054$), with levels being highest in 2009 (2008 had the lowest total rainfall and 2009 ended latest, although rainfall was distributed over fewer months). Overall, grazing reduced total vegetative cover ($F_{1,65} = 13.49$, $P = 0.0005$; Fig. 2) and increased bare ground ($F_{1,65} = 6.81$, $P = 0.0113$; Fig. 2).

Although we did not detect a significant effect of cattle grazing on the species richness of the seven plant groupings considered collectively ($F_{1,9} = 0.22$, $P = 0.67$; Table 2), grazing did have an overall significant effect on the percentage cover of these groups ($F_{7,59} = 1468.36$, $P < 0.0001$). As summarized in detail in Appendix S1, subsequent protected GLMs revealed that exotic annual grasses and exotic annual forbs were the major drivers of this MANOVA result. Cover of exotic annual grasses was significantly reduced by grazing ($F_{1,65} = 31.91$, $P < 0.0001$; Fig. 3a), with there being a trend for the impacts of grazing to vary among years ($F_{2,64} = 2.74$, $P = 0.07$). This latter interaction resulted from the effects of grazing being less pronounced in 2008 than in the other

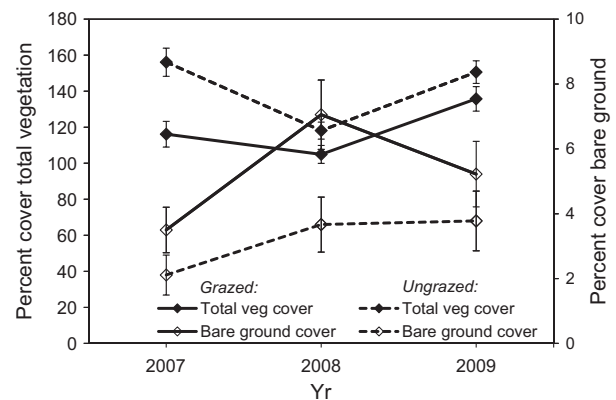


Fig. 2. Mean (± 1 SE) absolute percentage cover of (a) total vegetation and (b) bare ground as a function of cattle treatment (present, absent) and year (2007–2009).

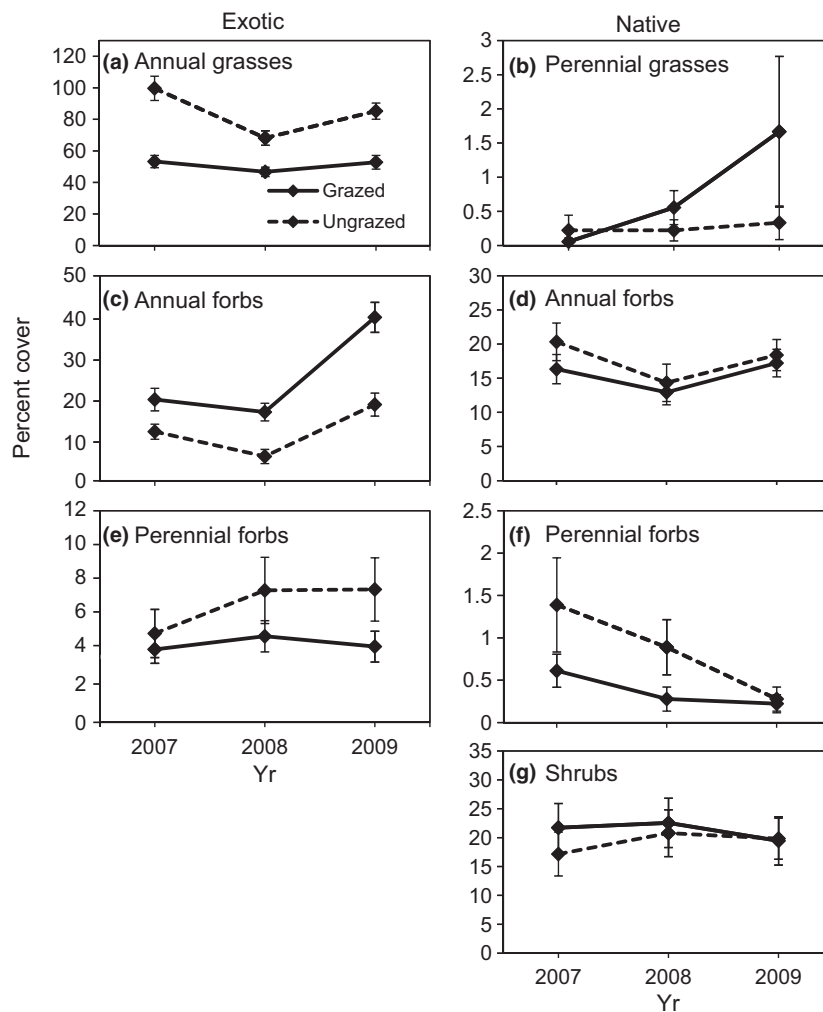


Fig. 3. Mean (± 1 SE) absolute percentage cover of seven plant groups as a function of cattle treatment (present, absent) and year (2007–2009): (a) exotic annual grasses, (b) native perennial grasses, (c) exotic annual forbs, (d) native annual forbs, (e) exotic perennial forbs, (f) native perennial forbs and (g) native shrubs.

2 years. In addition, we detected a significant three-way interaction among grazing, year and site ($F_{8,130} = 1.53$, $P = 0.0266$). Generally, cattle grazing caused the most dramatic reduction in the cover of exotic annual grasses in the first year of the study (2007) in all sites except for one, which experienced evenly increasing reductions each year.

In contrast to the results for exotic annual grasses, cattle grazing increased the cover of exotic annual forbs ($F_{1,65} = 33.67$, $P < 0.0001$; Fig. 3c). There was a trend for the effect of grazing on this group to increase in magnitude each year ($F_{2,64} = 2.13$, $P = 0.13$). In addition, there was a trend for grazing impacts to vary among sites, with increases in cover being higher at two sites than at the other three (grazing \times site interaction: $F_{4,65} = 1.91$, $P = 0.12$).

Grazing did not have a significant effect on the percentage cover of native perennial grasses ($F_{1,65} = 0.97$, $P = 0.33$), native annual forbs ($F_{1,65} = 0.08$, $P = 0.78$), native perennial forbs ($F_{1,65} = 1.21$, $P = 0.28$), exotic perennial forbs ($F_{1,65} = 0.59$, $P = 0.45$) or native shrubs ($F_{1,65} = 0.00$, $P = 0.99$). However, the effect of grazing on exotic perennial forbs varied significantly among sites (grazing \times site interaction: $F_{4,65} = 2.64$, $P = 0.0418$), with grazing having a negative effect on cover at two sites, no effect at one, and a positive effect at two others. We also detected a trend for the effect of grazing on native shrubs to vary among years ($F_{2,64} = 2.30$, $P = 0.11$), where effects diminished through time (Fig. 3g).

Grazing had substantial effects on the most dominant exotic plant species at our site, *B. diandrus*. The height of this invader was significantly reduced by grazing

Table 2. Mean number (± 1 SE) of plant species per plot, averaged across 3 years (2007–2009), as a function of cattle grazing treatment (grazed vs. ungrazed) and plant characteristics (geographic origin, life history and life form).

Plant group	Mean plant richness/plot	
	Grazed	Ungrazed
Exotic annual grasses	4.4 (0.2)	4.5 (0.2)
Native perennial grasses	0.5 (0.1)	0.3 (0.1)
Native annual forbs	10.6 (0.5)	10.3 (0.6)
Exotic annual forbs	6.1 (0.3)	5.8 (0.3)
Native perennial forbs	1.6 (0.2)	2.1 (0.2)
Exotic perennial forbs	1.2 (0.1)	1.2 (0.1)
Native perennial shrubs	3.2 (0.2)	3.0 (0.1)

($F_{1,4} = 163.86$, $P = 0.0002$; Fig. 4). Grazing also reduced spikelet production ($F_{1,4} = 12.99$, $P = 0.0226$; Fig. 4) and this effect varied among sites ($F_{4,450} = 1.29$, $P = 0.0015$), with the most dramatic reduction occurring at a single site.

Discussion

Results from our enclosure experiment indicate that cattle grazing substantially affected a coastal grassland community in central California by reducing overall plant biomass by 70% (Fig. 1) and altering relative dominance of plant groups (Table 1). Grazing caused a 40% reduction in the cover of exotic annual grasses (Fig. 3a), which were the most dominant group in this system, comprising over two-thirds of the vegetative cover. In addition, cattle reduced the size and fecundity of the most dominant of these species, *B. diandrus* (Fig. 4). In contrast, grazing caused a 15% increase in the cover of exotic annual forbs and had no effect on the cover of native perennial grasses, annual and perennial forbs or native shrubs (Fig. 3). Grazing did not affect the species richness of either native or exotic plant taxa.

Although cattle grazing had a strikingly negative effect on exotic annual grasses in our study, and this response is frequently hypothesized as a critical conservation benefit in mesic grasslands (Hayes & Holl 2003a), few studies in California have reported such effects. For example, in a non-experimental study comparing grazed and ungrazed coastal grasslands, Hayes & Holl (2003a) found the opposite effect, with cattle grazing associated with higher cover of exotic annual grasses in one of 2 years. Other studies have also shown that grazing can have positive effects on some species of exotic annual grasses (White 1967; Fossum 1990). Two possible explanations for these differences relate to the fact that the studies of Hayes, Holl and White involved comparisons of sites that were grazed or ungrazed for long periods. Therefore, their results may have captured long-term effects of cattle grazing or reflect initial

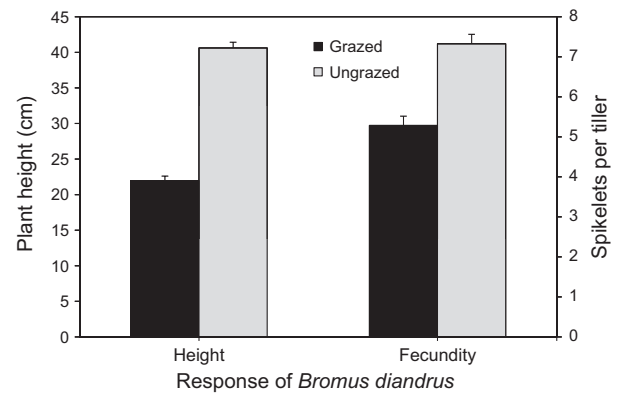


Fig. 4. Mean (± 1 SE) height (cm) and spikelet production per tiller for *Bromus diandrus* as a function of cattle treatment (present, absent).

differences among sites unrelated to grazing. Outside California, Golodets et al. (2009) also found that moderate and heavy cattle grazing reduced the biomass of tall annual grasses in arid grasslands of Israel.

Timing of grazing may play a role in explaining the negative impacts of cattle on exotic annual grasses in general and *B. diandrus* specifically. This grass, like many other exotic species, germinates very early in the growing season and this characteristic may contribute to its competitive success as a grassland invader (Abraham et al. 2009). We hypothesize that, by introducing cattle in late winter and early spring when exotic annual grasses were establishing, grazing substantially reduced the dominance of these invaders while having minimal effects on established native perennials and later-germinating native annuals. This strategy is often recommended (DiTomaso 2000) and research conducted on invaded grasslands in Montana found this to be the most beneficial practice (Rinella & Hileman 2009).

The reduction in cover of exotic annual grasses caused by cattle grazing was associated with an increase in the cover of exotic annual forbs, driven primarily by dramatic increases in *Erodium cicutarium* and *Hypochaeris glabra* (Table 1c). This response is similar to that found in other studies, including those in mesic coastal grasslands in California (Hayes & Holl 2003a; b) and more dissimilar systems in temperate and subtropical Australia (Prober & Thiele 1995; McIntyre & Lavorel 2001), Argentina (Facelli et al. 1989) and Europe (Lanta et al. 2009). McIntyre & Lavorel (2001) found that low-growing forbs were favoured by high-intensity grazing and taller, while more leafy forbs were favoured by low-intensity grazing. One hypothesis to explain our result is that exotic annual grasses are competitively dominant to exotic annual forbs and, in the absence of cattle grazing, suppress the abundance and cover of this less competitive group. Grazing may interrupt this

competitive dominance (Harper 1977; Rice 1989 and references therein) and create increased availability of space and resources, such as soil nutrients, water or light, which may drive the observed increase in exotic annual forbs. Surprisingly, exotic annual forbs were the only group to respond positively to major reductions in cover of the most dominant group in our system (i.e. exotic annual grasses). Exotic annual forbs are only one part of the plant community (comprising 20% of the total vegetative cover) and the observed increase in their cover (15%) due to cattle grazing was not proportional to the decrease in exotic annual grasses (40%). Indeed, cattle reduced total vegetative cover by 25% and increased bare ground by 40%. This indicates that cattle grazing created substantial openings in this grassland community that have yet to be colonized fully by other plant groups. Although repeated grazing may have prevented this colonization, we observed no marked germination or colonization of the bare spaces in mid- and late winter (when peak germination occurs), before cattle were introduced to the area. One hypothesis to explain this lack of response is that our site experienced a mild drought during the study period, with precipitation 25–35% below the 20-yr average. Other grassland studies from Europe, Asia and the Americas have shown that drought has marked effects on community composition and structure through reductions in productivity and altered competitive dynamics (Biondini et al. 1998; Loeser et al. 2007; Gilgen & Buchmann 2009), particularly when interacting with grazing disturbance (Adler et al. 2005; Heitschmidt et al. 2005; Gao et al. 2009).

In contrast to our original hypothesis, cattle grazing did not increase the richness or cover of native plant species during our 3-yr study. This is surprising given the 70% decrease in plant biomass and 40% decrease in cover of exotic annual grasses. One hypothesis to explain this result is that native species may possess traits that caused them to respond more slowly to grazing than exotic taxa. For example, 33% of the native, non-shrub species were perennial compared to 10% for exotic taxa. Perennial taxa may be more adversely affected by grazing or take longer to respond to openings in the community. An extensive meta-analysis by Díaz et al. (2007) supports this view, as they showed that grazing most frequently increased the abundance of annual plant species and decreased the abundance of perennials (also see Johnson & Cushman 2007). They also reported a trend for abundance of exotic plants to increase in response to grazing and abundance of natives to decrease. A second hypothesis to explain our results is that native species, particularly native annuals, are smaller in stature than the dominant annual grasses. While low-growing, rosette-forming exotic annuals *E. cicutarium* and *H. glabra* seemed well suited to grazing, the smaller but upright native annuals (e.g. *Madia elegans*)

were less successful. A third hypothesis to explain our results is that native seed banks may be so depleted (in species, propagules or both) that these taxa are unable to capitalize on the less competitive environments created by grazing. However, the continued presence of native annuals (12–22% cover) suggests that seed bank depletion is not a sufficient explanation for their lack of response (but see Seabloom et al. 2003), but may be a factor for native perennials (1–3% cover).

Although we did not detect an effect of grazing on cover or species richness of native groups (Table 2), other studies have shown that cattle have large impacts on these taxa. In contrast to our results, Bartolome et al. (2004) found that two California native perennial grasses (*Nasella pulchra* and *N. lepida*) were positively affected by cattle grazing, whereas another was negatively affected (*Danthonia californica*). They suggested, as do Dyer & Rice (1997), that some native perennial grasses benefit from grazing because they experience reduced competition from neighbouring annual grasses and forbs. Similarly, light cattle grazing increased perennial grass cover in Australia (McIntyre & Lavorel 2001). Hayes & Holl (2003a) reported that cover and richness of native annual forbs in California responded positively to cattle grazing, while native perennial forbs were negatively impacted. They hypothesized that the increase in native annual forbs was caused by decreased light competition and increased bare soil, but taller native perennial forbs were disadvantaged when exposed to grazing.

Although our community sampling detected only a trend for grazing to negatively affect shrub cover, which diminished through time (Fig. 3g), Graydon (2009) used more detailed sampling in our same enclosure experiment over 3 years and found that cattle significantly reduced the volume of the most dominant shrub, *Eriogonum parvifolium*. There was no evidence that cattle fed on the shrubs, so herbivory cannot explain this result. Instead, Graydon (2009) showed that physical damage by cattle was the primary means of negative impact on shrubs. In contrast to these results, the meta-analysis of Díaz et al. (2007) found that grazing had neutral effects on woody species. However, both Casasús et al. (2007) in the Mediterranean and Harrington & Kathol (2008) in the Midwestern USA documented that cattle grazing decreased the abundance and size of shrubs and can be an effective tool for reducing their encroachments.

A key issue in ecology is the degree to which plant groupings based on ecological characteristics can be used to describe how native and exotic components of communities respond to disturbances, such as grazing (Lavorel et al. 1997; Díaz et al. 2007). Specifically, it is not always apparent whether plant species in particular life-history and/or life-form groups respond similarly, as suggested by

such classification schemes. Table 1 provides details on the grazing responses of plant species from our different groupings. Overall, the classification scheme we used suited the plant community well. For example, our enclosure experiment showed that grazing significantly decreased cover of exotic annual grasses as a group (Fig. 3a), and Table 1 reveals that over 70% of the species in this group responded similarly. Only two species did not respond in the same direction as the group, but they collectively comprised less than 2% cover. Grazing also caused significant increases in the cover of exotic annual forbs (Fig. 3c), and 62% of the plant species in this group responded in the same direction. Five species exhibited different responses from the group, but again, they collectively comprised less than 2% cover. Other groups that did not exhibit significant responses to grazing were mainly comprised of species with very low (<1%) cover. For example, native annual forbs comprised 22 species, but only five of these had percentage cover values above 1%. These patterns suggest that grazing had proportionally higher impacts on species that were already more common in the study area.

The similarities in response direction described above not only support our a priori decision to assign plant species to particular groups, but also provide support for the idea that geographic origin of species per se influences the magnitude and direction of responses to grazing. Research indicates that invasive exotic plants have a particular suite of traits (beyond life-history and life-form distinctions) that distinguish them from their native counterparts, enabling them to be superior competitors. For example, a recent meta-analysis by van Kleunen et al. (2010) found that invasive, exotic plant species had higher values for performance-related traits (physiology, leaf area allocation, shoot allocation, growth rate, size and fitness) than confamilial or congeneric native, non-invasive species. Godoy et al. (2011) also found that among 20 invasive, exotic plant species, all had a higher capacity for carbon gain as well as increased performance across a wide range of resource availabilities than their native congeners.

Our enclosure experiment has shown that cattle grazing caused major changes in a coastal grassland community and that responses of native and exotic taxa with different life-history and life-form characteristics varied markedly. Grazing caused precipitous declines in overall biomass and cover of the most dominant group in this system – exotic annual grasses – as well as reductions in the performance of its most abundant member, *B. diandrus*. Exotic annual forbs were the only group to increase in response to these major changes, but did so much less than expected, given the reduced dominance of exotic annual grasses and increased availability of bare ground for colonization. In contrast, native grasses and forbs were unaffected by grazing to date and we have hypothesized that this is due to

either depleted seed banks or possession of life-history characteristics that cause slow responses to grazing. Regardless of the explanation, our research highlights the importance of comparing responses of different plant groups that vary in life-history and life-form characteristics and geographic origin. Understanding the responses of these divergent groups is not only important for basic research on the effects of herbivores on plant communities, but is also critical for developing science-based approaches for sustainably managing invaded grasslands. The key management issue remaining is whether additional years of cattle grazing will allow native grasses and forbs to respond positively to the large decrease in exotic annual grasses. If these native groups remain unresponsive, or if a more rapid response is desired, active restoration through seed supplementation may be necessary to increase native plant cover.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Results from a series of ‘protected’ repeated-measures GLMs evaluating the impact of cattle grazing and numerous other factors on absolute percentage cover of native and exotic plant taxa from different functional groups.

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