Differing Effects of Cattle Grazing on Native and Alien Plants

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Abstract: *Habitat managers use cattle grazing to reduce alien plant cover and promote native species in California grasslands and elsewhere in the western United States. We tested the effectiveness of grazing as a restoration method by examining the effects of herbivory on native and alien plants. At Carrizo Plain National Monument, California, we surveyed native and alien species cover in adjacent grazed and ungrazed areas. We also established experimental plots in which plants were clipped or mulch (dead biomass) was removed. In addition, we clipped plants grown in pots and plants in the field that grew with and without competitors. Native species were negatively affected by clipping in 1999, 2000, and 2001, whereas alien species were unaffected. In the experimental field plots, the European annual forb* Erodium cicutarium *compensated in growth and reproduction following simulated herbivory. In contrast, growth and reproduction of the native perennial bunchgrass* Poa secunda *were reduced 1 year after clipping. In pots,* E. cicutarium *overcompensated and grasses undercompensated. In the field, European grasses were unaffected by the removal of competitors. It is unclear by what mechanism* E. cicutarium *was able to compensate, but the ability may be related to its basal rosette growth form and indeterminately growing inflorescences. The native California grassland community assembled in the absence of grazing herds, whereas invasive European species have been exposed to grazing for centuries. It may be that these invaders have adaptations that better enable them to recover from grazing. In the grassland we studied, the strategy of livestock grazing for restoration is counterproductive. It harms native species and promotes alien plant growth.*

Key Words: California grassland, Carrizo Plain National Monument, *Erodium cicutarium*, invasive alien plants, native plant diversity, overcompensation

Diferentes Efectos del Pastoreo de Ganado sobre Plantas Nativas y Exóticas

Resumen: *El pastoreo de ganado es utilizado por las personas a cargo del manejo del hábitat para disminuir la cobertura de plantas exóticas en pastizales de California y otras áreas del occidente de Estados Unidos. Probamos la efectividad del pastoreo como un método de restauración examinando los efectos de la herbivoría sobre plantas nativas y exóticas. Muestreamos la cobertura de especies nativas y exóticas en áreas adyacentes con y sin pastoreo en el Monumento Nacional Carrizo Plain, California. También establecimos parcelas experimentales en las que las plantas fueron cortadas o la biomasa muerta fue removida. Adicionalmente, cortamos plantas cultivadas en macetas y plantas silvestres que crecieron con y sin competidores. Las especies nativas fueron afectadas negativamente por los cortes en 1999, 2000 y 2001, mientras que las especies exóticas no fueron afectadas. En las parcelas experimentales de campo, la hierba anual europea* Erodium cicutarium *compensó en crecimiento y reproducción después de la herbivoría simulada. En contraste, el crecimiento y reproducción del graminea perenne nativo* Poa secunda *disminuyeron 1 año después del corte. En macetas,* E. cicutarium *sobrecompensó y los pastos descompensaron. En el campo, los pastos europeos no fueron afectados por la remoción de competidores. No está claro el mecanismo mediante el cual* E. cicutarium *fue capaz de compensar, pero la habilidad puede estar relacionada con su forma de crecimiento de roseta basal e inflorescencias con crecimiento indeterminado. La comunidad de pastos nativos se configuró en ausencia del pastoreo de rebaños, mientras que las especies europeas invasoras han estado expuestas al*

pastoreo por siglos. Puede ser que los invasores tengan adaptaciones que les permiten recuperarse mejor del pastoreo. En el pastizal que estudiamos, la estrategia de pastoreo para la restauración es contraproducente. Perjudica a especies nativas y promueve el crecimiento de plantas exóticas.

Palabras Clave: diversidad de plantas nativas, Erodium cicutarium, Monumento Nacional Carrizo Plain, pastizales de California, plantas exóticas invasoras, sobrecompensación

Introduction

Massive invasions by alien plants have occurred throughout the western United States. In California's valley grasslands, a few annual species from the Mediterranean region, such as *Erodium cicutarium* and *Bromus madritensis* (botanical nomenclature follows Hickman 1993), have become the most abundant species (Wester 1981; Heady 1988; Menke 1990; Schiffman 2000), apparently outcompeting native annual wildflowers and perennial bunchgrasses (Schiffman 1994; Meyer 1997). In some of these grasslands, management plans employ cattle grazing to reduce the competitive advantage of alien species and to encourage native species (U.S. Bureau of Land Management 1996, 1998; Germano et al. 2001). To date, however, no long-term studies have addressed the effectiveness of cattle grazing as a restoration tool (Belsky & Gelband 2000). Here, we present data contrary to this management strategy and discuss the abilities of a few alien and native annual species to compensate for herbivory.

Large herbivores existed in California during the Pleistocene (Edwards 1990; Blumler 1992), but later the climate changed and a new flora assembled without the influence of grazing herds (Raven & Axelrod 1978). Native plant species extant in modern grasslands that also existed during the Pleistocene were exposed to grazing pressures by bison (*Bison*), horses (*Equus*), and mammoths (*Mammuthus*) that were similar to the pressures of modern cattle (*Bos*) grazing (Edwards 1990; Stock & Harris 1992). These species may have developed strategies to avoid or tolerate herbivory. Following the extinction of Pleistocene herbivores in California, however, grazing avoidance and tolerance were no longer advantageous (Blumler 1992).

Most studies of grazing effects in California focus on the native bunchgrass *Nassella pulchra* (Dennis 1989; Menke 1990; Huntsinger et al. 1996; Dyer & Rice 1997). These studies yielded conflicting results, either demonstrating that clipping reduces fitness (Dennis 1989; Huntsinger et al. 1996) or demonstrating increased fitness due to reduction of European grass cover (Nelson & Allen 1993; Dyer & Rice 1997; Gerlach et al. 1998). Plants exhibit diverse responses to herbivory, and these responses determine the effectiveness of grazing for restoration. Therefore, in addition to studying the effects of grazing on bunchgrasses, it is crucial to study the effects on native annuals because

annuals likely dominated southern California's historical (preinvasion) grasslands and still account for the majority of native species (Wester 1981; Hamilton 1997; Schiffman 2000).

When loss of live foliage has no net effect, it is because the plants compensate for tissue losses. In other cases, plants are negatively affected; in other words, they "undercompensate." Overcompensation, or an increase in productivity or fitness as a result of grazing (Owen & Wiegert 1981), has also been demonstrated in a few species (Paige & Whitham 1987; Hjalten et al. 1993; Lennartsson et al. 1997, 1998). In these cases, the probable compensatory mechanism was an increase in lateral growth following removal of the apical meristem (Paige & Whitham 1987; Hjalten et al. 1993; Lennartsson et al. 1997, 1998). Thus, the location of the apical meristem may be important in determining tolerance. Other traits that enable a plant to tolerate herbivory may also be reflected in the growth architecture of the plant (Strauss & Agrawal 1999).

After the Pleistocene extinctions of large herbivores in California, plants with the ability to overcompensate were probably negatively affected by the fitness costs of tolerance and were unable to reap the benefits of grazing-induced overcompensation. Such species probably became less important. In contrast, European species, particularly those originating in the Mediterranean region, experienced livestock grazing for thousands of years. Tolerance of intense herbivory may be an adaptive trait that is under selection in populations with prolonged exposure to large grazing herds (Lennartsson et al. 1997; Strauss & Agrawal 1999).

Native elk (*Cervus elaphus*), pronghorn antelope (*Antilocapra americana*), rodents, rabbits, and insects were, and still are, important herbivores in post-Pleistocene California grasslands, but they exert a different type of pressure on vegetation from that of domestic livestock (Painter 1995). Elk and pronghorn antelope are the most similar to cattle and the Pleistocene megafauna, but both species range much more widely than cattle, so their grazing effects are diffuse (Painter 1995). Likewise, small mammals and herbivorous insects produce a very different form of damage (Joern 1989). California's native grassland herbivores do not provide the predictable, severe defoliation that is necessary for tolerance to be adaptive (Lennartsson et al. 1997). Invasive European plant species arrived in California at the same time as the herds of

cattle (Heady 1988; Wagner 1989). Cattle were probably responsible for the dispersal of European seeds as they moved across California (Malo & Suarez 1995; Huntsinger et al. 1996). Thus, European plants, already adapted to grazing, were introduced into the native grassland community (Heady et al. 1992) at the same time intensive grazing commenced.

The effects of cattle grazing may include defoliation, removal of dead biomass, trampling, soil erosion, seed dispersal, and addition of manure and saliva. The removal of live foliage and dead biomass are the factors that have been said to aid native plants (U.S. Bureau of Land Management 1996, 1998). Most plants in this ecosystem grow during the winter rainy season and produce seed by early summer (Heady 1988; Heady et al. 1992). After reproduction, annual plants die and herbaceous perennials die back to their roots, or, in the case of bunchgrasses, their crown. The majority of biomass grows from the ground the following winter. Aboveground, mulch (thatch, litter, standing dead biomass) usually persists from the previous year. Most of this mulch is from alien grasses, and it may inhibit the germination and growth of native plants (Evans & Young 1989; Foster & Gross 1998; Reynolds et al. 2001). Cattle eat mulch along with living plants, so grazing is said to be beneficial in part due to mulch removal (Heady 1956). Thus, mulch removal as well as consumption of live foliage could shift the competitive hierarchy in favor of or against natives.

We focused on two important grazing effects, loss of living tissues and removal of mulch. We examined the consequences of these effects on native and alien species in a California valley grassland at Carrizo Plain National Monument. Our goals were to (1) determine whether native and alien species respond differently to grazing and, specifically, how cover and diversity are affected; (2) examine how simulated grazing affects growth and reproduction in the native perennial bunchgrass *Poa secunda*; and (3) determine whether simulated grazing induces compensatory growth in native and alien plants reared in pots without competition and under more natural field conditions with and without competition from neighboring plants.

Methods

Field Census

Carrizo Plain National Monument includes the largest remnant of the once vast California valley grassland. We selected a study site there that supported a large proportion of native species, including the bunchgrass *Poa secunda*. It also had a lower cover of European grasses than the rest of the area (Kneitel 1997; Meyer & Schiffman 1999). An examination of a series of aerial photographs (1936–2000) indicated that it was never cultivated.

In February 1990, grazing within a portion of the study area was halted because of the presence of two endangered plants, *Caulanthus californicus* and *Lembertia congdonii*. Grazing continued in the surrounding grassland. In April 2001 we recorded all plants intercepting 1000 random points on each side of the grazing fence. The points were located at least 200 m away from the fence. Cattle were not present on the grazed side of the fence during the year of sampling, although the area had been grazed in the spring of 2000 and in most previous years. We estimated the percent cover for each species from these data.

Field-Clipping and Mulch-Removal Experiment

In the fall of 1999, we established 50 plots of 1 × 1 m inside the grazing exclosure. We positioned the plots in a rough grid, avoiding rodent-caused soil disturbances (Schiffman 1994). There were 10 blocks of five treatments: controls (unclipped with mulch left intact), clipped once (late February), clipped twice (late February and early March), clipped three times (late February, early March, and early April), and mulch removed (late February, no clipping of live plants). We applied the treatments in the spring of 1999, 2000, and 2001, and clipping was done 1 cm above ground level (Orodho et al. 1998; Kotanen & Bergelson 2000).

Each year, a few weeks following treatment, we gathered data from a centrally located 0.25-m^2 (0.5 × 0.5 m) quadrat within each plot. We recorded all species found in the quadrat and estimated their covers by placing a wire grid over the quadrat and recording the species that intercepted each of 36 crossing points. We gave species present without intercepting a crossing point a cover value of 1%. We also determined relative percent cover of native species and total species evenness (Pielou 1969). Prior to treatment in March 2001, we determined the number of *P. secunda* inflorescences per individual and the height of the five tallest individuals in each plot.

We used a complete block design with two planned tests for this experiment. For parametric dependent variables—number of native species, total cover of native species, and relative cover of native species—we assessed clipping intensity with two-way mixed-model analysis of variance (ANOVA) with 27 df for error, 9 df for block, and 3 df for treatment. We analyzed the mulch-removal data similarly, with 9 df for error, 9 df for block, and 1 df for treatment (equivalent to a paired *t* test). For dependent variables that did not meet the assumptions of ANOVA, we analyzed clipping level with a Friedman's block test and mulch removal with a Wilcoxon signed-rank test.

We described the growth form and inflorescence architecture of each dominant species and assessed the potential for apical meristem damage. The slope of the relative cover for all control and clipped plots were averaged over 3 years to generate an index of the degree of compensation. The relative cover of each species was calculated by

dividing its cover by the average cover in all control and clipped plots.

Compensation-in-Pots Experiment

We germinated seeds of *Vulpia microstachys* (native annual grass), *Uropappus lindleyi* (native annual forb), *B. madritensis* (European annual grass), and *E. cicutarium* (European annual forb) on moist filter paper and planted individual seedlings in soil-filled PVC tubes (height 130 cm, diameter 5 cm) in January of 2001. Treatments included unclipped controls, plants clipped 1 month following planting, and plants clipped both 1 and 2 months following planting. The plants were different sizes before the first clipping, so before assigning them to treatments we blocked them into similar-size triplets (Maschinski & Whitham 1989). We randomly assigned treatments within each triplet.

We recorded the numbers of flowers or fruits in May, 1 month following the last clipping. We dried and weighed all the clipped material and, at the end of the experiment, we clipped the plants to ground level. We summed total aboveground productivity across all clippings, including final harvest, at the end of the pots experiment. We determined the effect of treatment on total productivity and unclipped reproduction with a two-way, mixed-model ANOVA, with block (size) as a random factor.

Field-Compensation Experiment

We selected individual seedlings of *B. madritensis*, *Vulpia myuros* (alien annual grass), *E. cicutarium*, and *Tripidocarpum gracile* (native annual forb) at random in the same grazing exclosure used for the field-clipping and mulch-removal experiment. We randomly assigned each seedling to one of four treatments in a 2 × 2 factorial design. The factors were unclipped or clipped and unweeded or weeded. We applied each treatment within a radius of 5 cm around each focal plant and removed all potential competitors (including conspecifics) from the weeded plants with forceps. At the end of the growing season we determined the number of developing fruits and the aboveground dry weight of each focal plant. We $\log(Y+1)$-transformed and analyzed the data with two-way fixed-factor ANOVAs.

Results

Field Census

The census on the ungrazed side of the fence yielded 5 alien and 24 native species (Fig. 1). The total native cover was 49%, and the total alien cover was 57%. The alien forb *E. cicutarium* was the most abundant species, followed by the native perennial bunchgrass *P. secunda*. The grazed side of the fence had 1 additional alien species and only half as many native species as the ungrazed area. The total

native cover in the grazed area was 46%, and the total alien cover was 79%. *Erodium cicutarium* was also the dominant species in this area, but it was followed closely by *Pectocarya penicillata*. No bunchgrasses occurred in the grazed area (Fig. 1).

Field-Clipping and Mulch-Removal Experiment

In each of the 3 years of the experiment, clipping one to three times significantly decreased the percent cover of native species. In contrast, the cover of alien species was unaffected in 2000 and 2001 and only decreased slightly after being clipped two or three times in 1999 (Fig. 2). The decrease in native species cover was highly significant in 1999 ($p < 0.00001$), 2000 ($p < 0.00001$), and 2001 ($p < 0.00001$). The relative cover of native species was also affected negatively by clipping (Fig. 2). This effect was significant in 1999 ($p = 0.00076$), 2000 ($p = 0.00004$), and 2001 ($p = 0.00001$). These clipping effects increased with the number of clippings (Fig. 2).

Native species richness was affected negatively by clipping, and this effect was significant in 1999 ($p = 0.00191$), 2000 ($p < 0.00001$), and 2001 ($p = 0.00176$). Native species richness continued to decrease with additional clipping (Fig. 2). Alien species richness was unaffected by clipping. Native species evenness changed significantly with clipping in all 3 years (Fig. 2). Specifically, clipping once or twice increased evenness in 1999 ($p = 0.06566$) and in 2000 ($p = 0.00690$). In 2001 all clipping treatments increased evenness ($p = 0.00003$).

The negative effects of clipping on native species were particularly evident in some of the more abundant species (Table 1). For example, *P. secunda* was affected negatively by clipping. The percent cover of this dominant native decreased with clipping in all 3 years of the study (Table 1). There were also residual effects of clipping on both the height and number of inflorescences per *P. secunda* individual prior to treatment in 2001 (Fig. 3).

Native forbs such as *Dichelostemma capitatum* and *Lepidium nitidum* suffered decreases in cover after clipping, as did the native grass *V. microstachys* (Table 1). In fact, the cover of all native species decreased following clipping. In contrast, the abundant alien species were generally unaffected by this treatment. Mean percent cover of *E. cicutarium* was greater, though not significantly, after several of the clipping treatments in 1999, 2000, and 2001 (Table 1). *Bromus madritensis* was unaffected by clipping (Table 1). The amount of bare ground increased significantly with clipping in all 3 years ($p < 0.0001$).

Growth architecture determined each species' response to clipping. Native forbs growing close to the ground and with indeterminate inflorescences were less affected by clipping than more upright species (Table 2). For example, *E. cicutarium* and *T. gracile* both have apical meristems at the soil surface, and they were both unaffected by clipping. *Lotus humistratus* and *P. penicillata* have prostrate growth forms and indeterminate
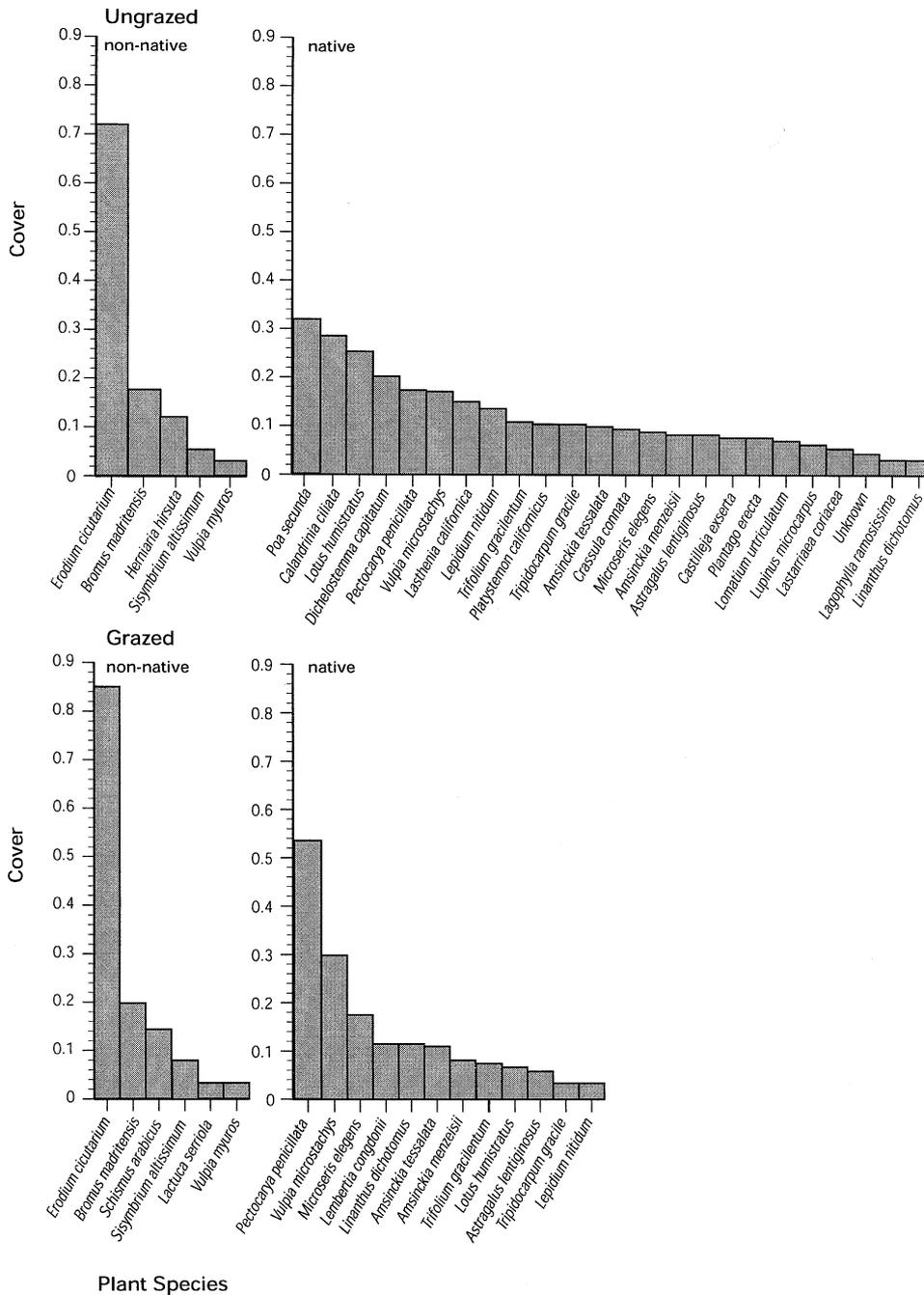
Figure 1. Dominance and diversity distributions for non-native and native plant species in an area protected from grazing since February 1990 (ungrazed) and an area grazed up to the previous year (grazed).

inflorescences of many branching stalks. They were not as negatively affected by clipping as the more upright-growing *Lasthenia californica* and *Castilleja exserta* (Table 2).

The response to mulch removal was inconsistent across years (Fig. 2). Native species cover decreased significantly in 1999 ($p = 0.00653$) and 2000 ($p = 0.01532$) but was unaffected in 2001 ($p = 0.75889$). Non-native cover was unaffected by mulch removal in all 3 years. The relative cover of native species decreased significantly with mulch removal in 1999 ($p = 0.00943$), decreased marginally in 2000 ($p = 0.07654$), and was unaffected in 2001 ($p = 0.85915$). Native species richness was not significantly

affected by mulch removal in 1999 ($p = 0.34344$), 2000 ($p = 0.48256$), or 2001 ($p = 0.25755$). Nor was there a significant effect on native evenness (Fig. 2) in 1999 ($p = 0.71068$), 2000 ($p = 0.93383$), or 2001 ($p = 0.50116$). The cover of *Poa secunda* and *E. cicutarium* was not significantly affected by mulch removal (Table 1). However, *V. microstachys* was negatively affected. *Bromus madritensis* was not affected by mulch removal in 1999 or 2000 but was negatively affected in 2001 (Table 1).

Compensation Experiments

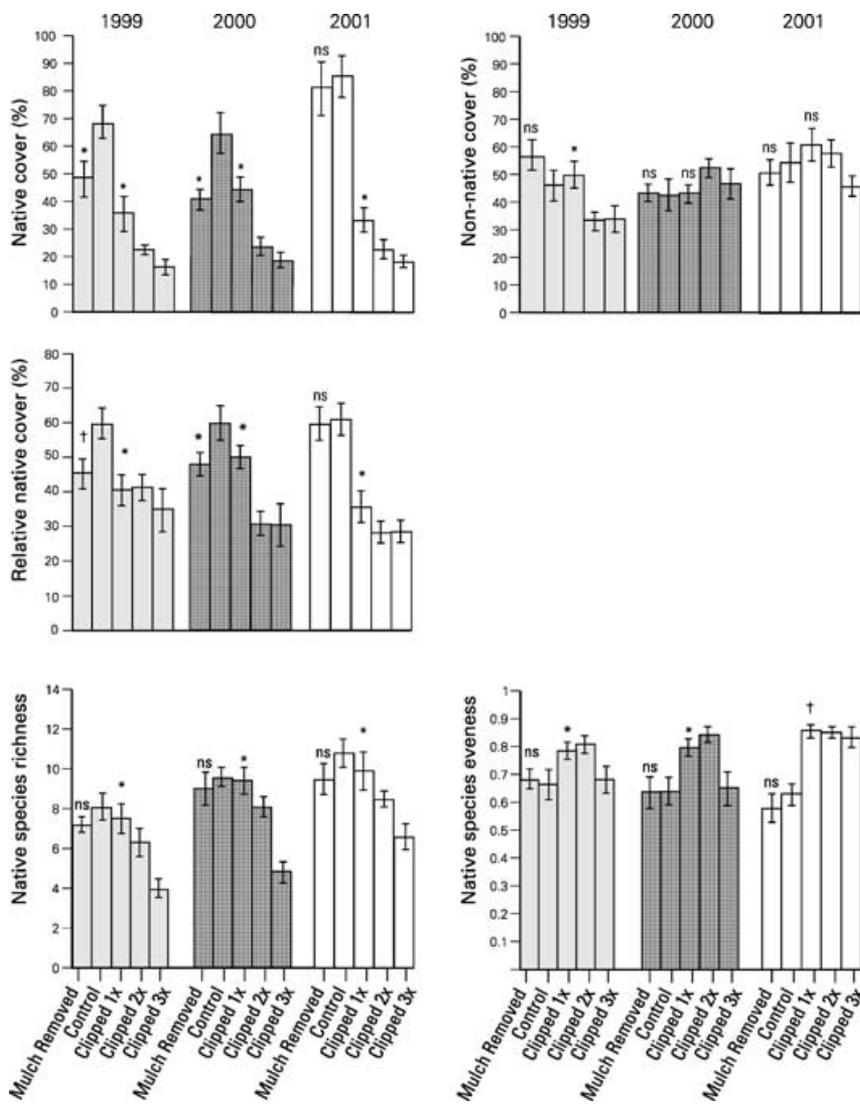*Erodium cicutarium* compensated for simulated herbivory when grown in pots. At final harvest, the number

Figure 2. Native cover, non-native cover, relative native cover, native species richness, and native species evenness for the field experiment on the effects of clipping and mulch removal in 1999, 2000, and 2001. Different years are indicated with differently shaded bars. Significance tests show two planned comparisons: control versus mulch removal and control versus three levels of clipping (control, 1×, 2×, and 3×). Values are means ± SE (n = 10; ns, p > 0.1, †, 0.1 > p > 0.05, *p < 0.05).

of flowers and fruits produced by clipped plants was not different from that of the control plants ($p = 0.6873$; Fig. 4). In terms of total productivity, *E. cicutarium* overcompensated ($p = 0.0001$). The number of individual flowers was not counted for the native composite *Uropappus lindleyi*, but the number of inflorescences produced by clipped plants was not significantly lower than the number produced by control plants ($p = 0.1082$; Fig. 4). The total productivity of *U. lindleyi* was not significantly affected by clipping ($p = 0.1182$). In contrast, grass species were unable to fully compensate following clipping (Fig. 4). *Bromus madritensis* decreased in flower production ($p = 0.0016$) and total productivity ($p = 0.0005$) following clipping. Clipped *V. microstachys* plants also had significantly fewer flowers ($p = 0.0041$) and lower total productivity than the controls ($p = 0.02497$).

In the field, *E. cicutarium* was negatively affected by clipping and positively affected by weeding (weight: clip-ping $p = 0.0087$, weeding $p = 0.0002$; fruits: clipping $p = 0.0283$, weeding $p = 0.0022$, Fig. 5). For *T. gracile*, there were no significant effects (weight: clipping $p = 0.2380$, weeding $p = 0.7553$; fruits: clipping $p = 0.2284$, weeding $p = 0.8658$). Productivity of the alien grasses *V. myuros* and *B. madritensis* was negatively affected by clipping, whereas weeding had no effect (Fig. 5). Fruit production of *V. myuros* was significantly less with clipping and unaffected by weeding. There was a marginally significant interaction between clipping and weeding for the number of *B. madritensis* fruits, so that interaction was not pooled (for *V. myuros* weight: clipping $p < 0.00001$, weeding $p = 0.7504$; fruits: clipping $p = 0.0016$, weeding $p = 0.2131$; for *B. madritensis* clipping × weeding interaction: $p = 0.0499$). *Bromus madritensis* was more affected by clipping when grown without competitors (Fig. 5). In all other cases, interactions were not significant and were dropped from the ANOVAs.

Table 1. Native and alien plant species, in order of abundance, found in 20 or more of the 50 clipping and mulch-removal experimental plots in 1999, 2000, and 2001.

Year and species	Control vs. mulch removal (p)[a]	Mulch removed[b]	Control[b]	Clipped[b]			Control vs. clipping (p)[c]
				1x	2x	3x	
1999							
alien							
Erodium cicutarium	0.234	49.06	40.63	41.88	30.94	30.31	0.098
Bromus madritensis	0.285	4.89	2.70	3.23	1.24	1.66	0.528
Herniaria hirsuta	0.623	3.01	1.96	3.43	0.93	1.45	0.804
native							
Poa secunda	0.959	21.88	21.25	10.00	7.29	4.69	0.020
Vulpia microstachys	0.007	6.98	25.94	10.63	1.45	4.48	0.005
Chorizanthe uniaristata	0.160	4.68	2.28	2.59	2.70	3.31	0.993
Dichelostemma capitatum	0.066	2.80	3.74	3.64	1.24	0.00	0.019
Lasthenia californica	0.994	4.05	4.79	0.94	0.40	0.10	0.290
Plantago erecta	0.497	1.03	2.08	2.18	2.50	1.03	0.703
Lepidium nitidum	0.916	1.04	1.86	0.51	1.56	0.10	0.682
2000							
alien							
Erodium cicutarium	0.726	42.22	40.28	41.39	49.17	45.83	0.204
Bromus madritensis	0.732	1.11	2.14	1.59	3.26	0.38	0.085
native							
Poa secunda	0.813	23.61	23.06	15.56	6.11	9.37	0.036
Vulpia microstachys	0.009	1.97	19.82	6.11	0.86	3.91	0.021
Dichelostemma capitatum	0.634	2.70	2.90	2.70	3.89	0.00	0.037
Uropappus lindleyi	0.115	1.11	3.81	1.77	2.32	0.00	0.082
Crassula connata	0.051	0.76	2.98	2.32	1.77	0.00	0.035
Calandrinia ciliata	0.777	1.69	1.51	2.80	1.41	0.28	0.040
Lepidium nitidum	1.000	1.08	1.33	2.44	1.79	0.28	0.025
Trifolium gracilentum	0.066	1.23	0.58	1.87	1.79	0.58	0.090
Lotus humistratus	0.783	1.53	1.43	1.51	0.40	0.78	0.171
Chorizanthe uniaristata	0.257	0.58	0.30	1.13	0.50	1.18	0.102
2001							
alien							
Erodium cicutarium	0.953	48.61	50.00	57.78	55.83	44.72	0.703
Bromus madritensis	0.018	0.48	2.70	0.78	0.68	0.20	0.119
Herniaria hirsuta	0.916	1.03	1.13	1.06	0.66	0.20	0.226
native							
Poa secunda	0.444	48.61	44.27	7.78	3.46	4.64	0.002
Lotus humistratus	1.000	8.48	8.61	3.81	4.01	4.44	0.052
Trifolium gracilentum	0.932	2.07	3.26	2.04	1.97	1.69	0.999
Lasthenia californica	0.723	3.71	4.29	1.69	0.40	0.38	0.577
Allium hyalinum	0.122	2.14	4.54	1.87	0.96	0.00	0.005
Calandrinia ciliata	0.606	2.52	0.96	2.42	2.42	0.86	0.165
Pectocarya penicillata	0.395	1.49	0.86	3.53	0.96	1.97	0.477
Uropappus lindleyi	0.203	0.78	2.70	2.44	1.51	0.96	0.283
Chorizanthe uniaristata	0.048	0.60	2.60	1.71	1.71	1.16	0.910
Lepidium nitidum	0.279	1.69	0.86	1.33	1.97	0.58	0.430
Dichelostemma capitatum	0.677	1.69	1.51	1.03	0.48	0.00	0.043

[a]*Control and mulch-removal treatments were compared using Wilcoxon signed-rank test.*
[b]*Mean percent cover (n = 10) for each experimental treatment.*
[c]*Control and clipping treatments were compared using Friedman's block test.*

Discussion

Effects of Grazing on Community Composition

In the field-clipping experiment, the negative effect of grazing on native plant diversity was evident after just one clipping, suggesting that the presence or absence of herbivores rather than the intensity of herbivory de-termined community composition. The field census on both sides of the grazing fence was unreplicated, but the results corroborated the results of the clipping experiment, adding strength to the finding that grazing causes a decrease in native plant diversity in this grassland (Fig. 2). Many of the species most negatively affected by clipping were absent from the grazed side of the fence in the field census. For example, *P. secunda*, *L. californica*,
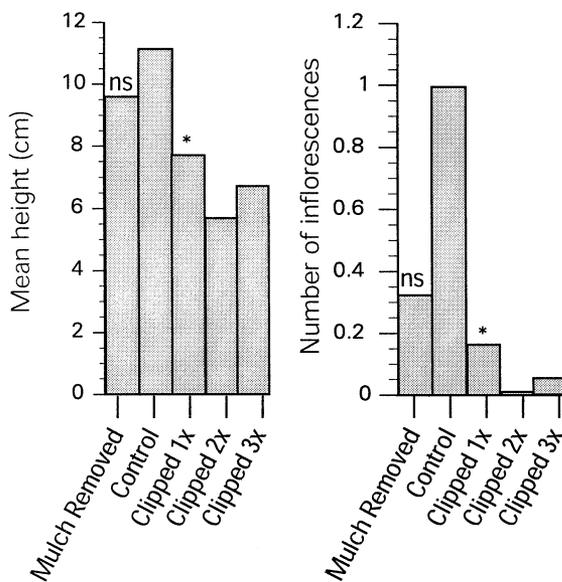
Figure 3. Mean height of the five tallest Poa secunda *individuals in each field plot and the number of inflorescences per individual following 2 years of treatment and prior to treatment in February 2001. The control and mulch-removal treatments were compared using Wilcoxon signed-ranks test. The control and clipping treatments were compared using Friedman's block test. Values are medians (*n = 10; ns, p > 0.1, †, 0.1 > p > 0.05, *p < 0.05).*

and *C. exerta*, all negatively affected by clipping in the field-plot experiment, were also abundant on the un-grazed side of the fence but undetected on the grazed side of the fence in the field census. Other native species whose cover decreased with clipping included the annual grass *V. microstachys* and the wildflowers *D. capitatum* and *Platago erecta*.

The increase in species evenness with clipping reflected a grazing-caused loss of localized, rare native species (Fig. 2). Other studies have demonstrated that abiotic factors including soil moisture levels interact with grazing pressures to influence community composition (Proulx & Mazumder 1998; Stohlgren et al. 1999; Safford & Harrison 2001). Carrizo Plain National Monument is a dry environment with precipitation totaling only 17.7, 13.1, and 14.6 cm in 1999, 2000, and 2001, respectively (National Oceanic and Atmospheric Administration 1999, 2000, 2001). Olff and Ritchie (1998) suggest that grazing in arid grasslands could increase extinction rates. In addition, areas with inherently low productivity, like the Carrizo Plain, would be expected to favor drought-tolerant plants that do not experience the grazing-induced release from competition observed in more mesic ecosystems (Olff & Ritchie 1998; Proulx & Mazumder 1998).

The effect of grazing may be understood by examining the role of the native perennial bunchgrass *P. secunda*

in the ecosystem as a whole. Although the historical importance of bunchgrasses in the California grasslands of pre-European settlement has been a subject of debate (Wester 1981; Heady 1988; Hamilton 1997; Schiffman 2000), the negative effects of simulated grazing on *P. secunda* suggest this species was more abundant in California's arid grasslands prior to the initiation of cattle grazing. Other native bunchgrasses, such as *Nassella pulchra* and *Achnatherum hymenoides* (*Oryzopsis hymenoides*), are sometimes negatively affected by grazing (Huntsinger et al. 1996; Orodho et al. 1998) and compete poorly with European grasses (Nelson & Allen 1993; Dyer & Rice 1997; Gerlach et al. 1998). Native forbs are also often excluded by invasive European grasses, partially because the European species reduce soil moisture levels (Welker & Menke 1990). In contrast, native bunchgrasses do not competitively exclude native forbs because of their growth form, which allows open space for forb growth (Carlsen et al. 2000).

Nassella pulchra seedlings have greater survival rates in grazed areas as a result of release from European grass competition (Dyer & Rice 1997). However, more mature *N. pulchra* plants are negatively affected by grazing, and no life stage can withstand heavy grazing (Dyer et al. 1996). The bunchgrass we examined, *P. secunda,* has an earlier growth and reproductive phenology than *N. pulchra*. In *P. secunda*, vegetative growth is initiated with the first winter rains and flowering occurs in early spring, sometimes even before that of *E. cicutarium* (Sampson & Chase 1927). This explains why our spring simulated-grazing treatments affected *P. secunda* growth and reproduction so negatively.

Erodium cicutarium was by far the most abundant species at our field site, on both the grazed side of the fence and in the area protected from grazing (Table 1; Fig. 1). It was not affected by clipping in the field plots, and when grown in pots its growth overcompensated following clipping (Fig. 4). These results are illustrative of the difficult problem this alien species poses. It is a fierce competitor, producing many seeds that germinate early, developing a deep tap root quickly, depleting soil water, and preventing sunlight from reaching seedlings of other species that germinate later (Bartolome 1979; Heady et al. 1992). It may prevent establishment of perennial grasses by blocking access to light (Menke 1990).

Contrary to expectations, mulch removal, another aspect of cattle grazing, had a negative effect on the cover of native species in 1999 and 2000 (Fig. 2). It simply may have been that the removal of mulch by hand represented a type of disturbance that harms native plants. Compared with other California grassland sites (Meyer & Schiffman 1999), however, the European grasses responsible for mulch (Heady 1956; Robles & Chapin 1995) were not too abundant at our field site. The relatively small amount of accumulated mulch may have actually been close to pre-invasion level and may have

Table 2. Growth characteristics and clipping responses of dominant plant species in experimentally clipped field plots at Carrizo Plain National Monument.

Species	Plant form and longevity	Potential for meristem damage	Vegetative growth form	Reproductive architecture	Response to clipping*
Alien					
Erodium cicutarium	annual forb with taproot	low	basal rosette	many branching stalks with indeterminate axillary umbels	−0.03
Bromus madritensis	annual grass	low	intercalary meristems	dense determinate panicle	−0.37
Native					
Poa secunda	perennial bunchgrass	low	intercalary meristems	many panicles, each of ± fixed size	−0.56
Vulpia microstachys	annual grass	low	intercalary meristems	few racemes, each of ± fixed size	−0.84
Dichelostemma capitatum	perennial geophyte	low	underground intercalary meristem	few determinate inflorescences	−0.54
Tropidocarpum gracile	annual forb with taproot	low	basal rosette	many branching stalks with indeterminate axillary flowers	−0.21
Lotus humistratus	annual forb with taproot	high	prostrate spreading, mostly cauline leaves	many branching stalks with indeterminate axillary flowers	−0.11
Calandrinia ciliata	annual forb with taproot	high	basal rosette	several inflorescences with axillary flowers	−0.18
Pectocarya penicillata	annual forb with taproot	high	prostrate spreading, mostly cauline leaves	many branching stalks with indeterminate axillary flowers	−0.28
Uropappus lindleyi	annual forb with taproot	moderate	basal rosette, upright leaves	one to few determinate composite heads	−0.33
Plantago erecta	annual forb with taproot	moderate	basal rosette, upright leaves	few determinate inflorescences	−0.28
Lepidium nitidum	annual forb with taproot	high	upright, mostly cauline leaves	few ± determinate inflorescences	−0.23
Castilleja exserta	annual forb with fine roots	high	upright, unbrancheed, mostly cauline leaves	one to few determinate inflorescences	−0.42
Lasthenia californica	annual forb with fine roots	high	upright, unbranched, mostly cauline leaves	one to few determinate composite heads	−0.92

Response to clipping is an index of the degree of compensation. A value of 0 indicates equal compensation, negative numbers indicate undercompensation, and positive numbers indicate overcompensation. The index is the slope of the relative cover for all control and clipped plots averaged over 3 years. Relative cover for each plot type was calculated by dividing the cover for that species by the average cover in all control and clipped plots.

benefited native plants by shading and preventing loss of soil moisture (Evans & Young 1989; Reynolds et al. 2001).
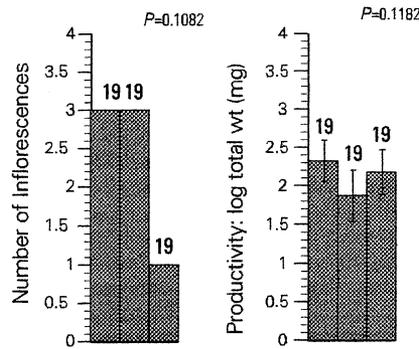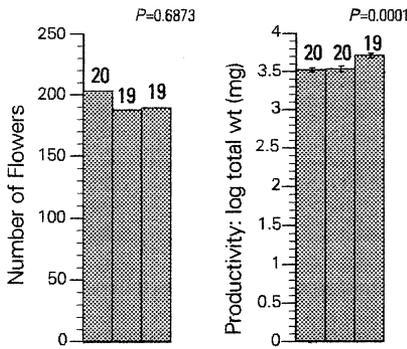
Cattle grazing may temporarily reduce mulch and the cover of European species such as *B. madritensis*, but it also reduces native cover and increases the amount of bare ground. This bare ground provides open space for the regeneration of alien plants such as *E. cicutarium* and for highly competitive annual grasses. Herbivory on a large scale ultimately selects for species more tolerant of grazing (Olff & Ritchie 1998). In the case of many grasslands in the western United States, these tolerant species are aliens.

Growth Architecture

Specific growth characteristics may be most closely tied to the ability of plants to tolerate herbivory and compensate for tissue losses (Crawley 1983; Strauss & Agrawal 1999). Comparisons of plant growth forms (Table 2) may explain the degree of compensation while demonstrating which morphological characteristics allow plants to tolerate herbivory (Strauss & Agrawal 1999). In grazed areas, species-sorting should favor species with such morphological attributes. For example, the compensatory ability we observed in *E. cicutarium* may be due to its basal rosette of leaves and gradual modular production of seeds.
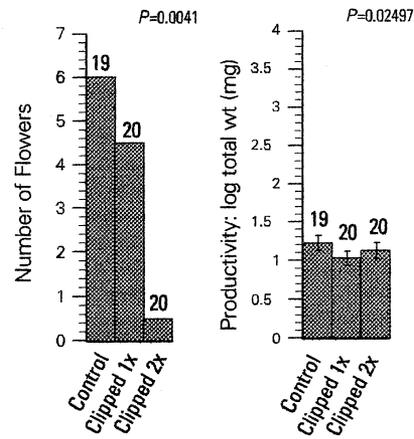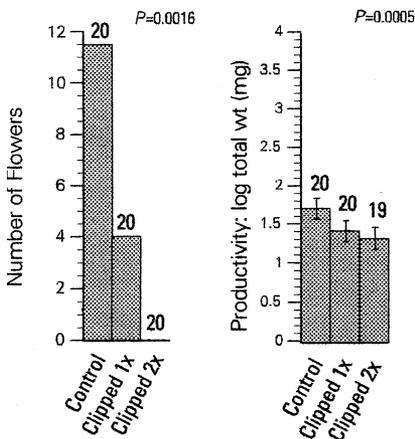
Figure 4. *Reproduction and productivity at the end of the experiment on the effects of clipping on four different species grown in pots. Reproduction values are medians, and reproduction probability values are from Friedman's block tests. Productivity is summed across all clippings. Productivity values are means ± SE, and productivity probability values refer to the treatment effect from a two-way, mixed-model analysis of variance. Sample sizes are indicated above the bars.*

Its principal apical meristem is located at the soil surface and is not damaged by clipping. Furthermore, its inflorescences grow constantly and indeterminately in axillary umbels, and when they are removed other inflorescences quickly replace them and rapidly resume seed production (Table 2). The native *T. gracile* has the growth form most similar to that of *E. cicutarium*. It was not as negatively affected by clipping as most other native forbs in the field
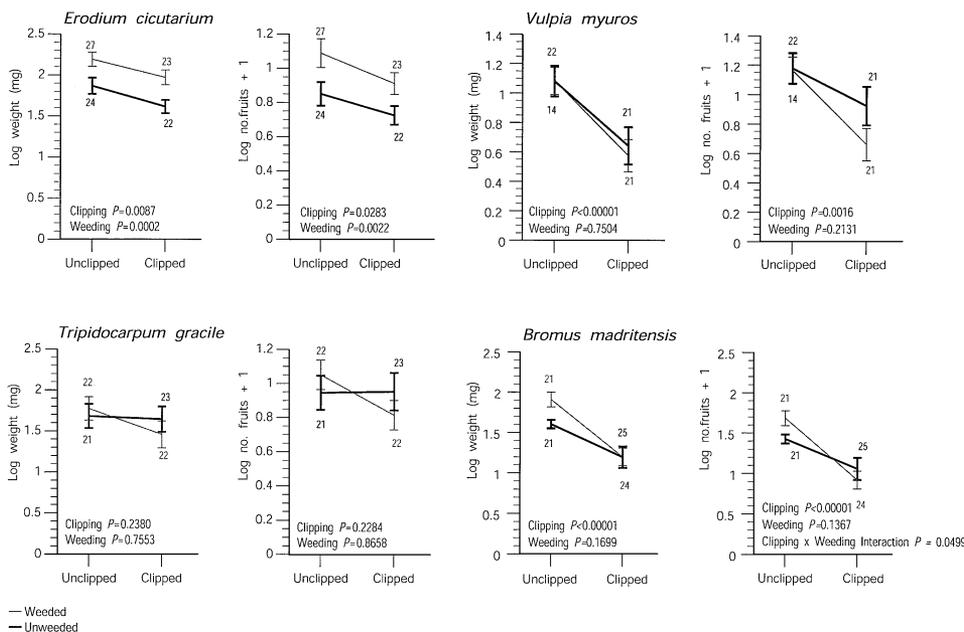
Figure 5. *Effects of clipping and weeding on four different plant species' growth and reproductive compensation in the field. Probability values refer to two-way analysis of variance. Values are means ± SE, and sample sizes are indicated above the bars.*

— Weeded
— Unweeded

plots (Tables 1 & 2), and it was able to compensate in the field, both with and without competition (Fig. 5). As with *E. cicutarium*, the principle meristem in *T. gracile* is located at the soil surface, escaping grazing damage, so its modular indeterminant inflorescences recover rapidly.

Native forbs growing close to the ground and with indeterminate inflorescences were less affected by clipping than the more upright species. For example, *Lotus humistratus* and *Pectocarya penicillata* were not as negatively affected by clipping as *Lasthenia californica* and *Castilleja exerta*, which grow upright and have only a few determinate inflorescences (Table 2). Neither upright species was able to recover from this damage. *Uropappus lindleyi*, which has a basal rosette and apical meristem close to the soil surface, was able to compensate for herbivory when grown in pots, but its cover was negatively affected by clipping in the field plots. Its architecture may allow it to recover from clipping under ideal conditions (Tables 1 & 2; Fig. 4). *Lotus humistratus* and *P. penicillata* occurred in the grazed area of the field census, another indication that their growth form enables them to tolerate herbivory (Table 2; Fig. 1).

Morphological differences were also found between plants inside and outside a grazing exclosure in South Dakota (Painter et al. 1989) and on either side of a grazing fence in South Africa (Todd & Hoffman 1999). Likewise, in an Australian grassland, prostrate plants with meristems located at or below ground level were more common in a grazed area, and species with upright growth were more common in an ungrazed area, suggesting that certain morphological characteristics enable plants to tolerate herbivory and that other attributes help plants be superior competitors (Tremont 1994).

Physiological Contingency of Compensation

The degree of tolerance to herbivory is influenced by environmental conditions, competition, and the time of defoliation (Maschinski & Whitham 1989; Bergelson & Crawley 1992). Compensation is most likely to occur under favorable growth conditions. In our pot-compensation experiment, plants were not limited by competition, water, or resources. Under these conditions, the plants were more likely to compensate for herbivory. *Erodium cicutarium* compensated for herbivory in terms of the number of flowers and overcompensated in terms of total aboveground productivity (Fig. 4). In the field-compensation experiment, where conditions were harsher, *E. cicutarium* was negatively affected by clipping (Fig. 5). In *U. lindleyi*, inflorescence number decreased after two clippings, but this reduction was not significant (Fig. 4). Like *E. cicutarium*, *U. lindleyi* responded negatively to clipping in the field plots. Its ability to compensate in pots may also have been due to the favorable growing conditions (Table 1; Fig. 4). Both alien *B. madritensis* and native *V. microstachys* were nega-

tively affected by clipping in the pot experiment (Fig. 4). However, the seedlings of these two grasses seemed somewhat harmed when planted in pots at the beginning of the experiment. Therefore, their responses to clipping in pots may not reflect ideal growing conditions.

Some plant species are less likely to compensate for herbivory when they are grown with competition (Maschinski & Whitham 1989; Hjalten et al. 1993). However, the alien grasses *B. madritensis* and *V. myuros* were both unaffected by weeding, indicating their superior competitive abilities. Individuals of these two grasses were unable to compensate for herbivory, but the cover of these plants was unaffected by clipping in the field plots and was similar on both sides of the grazing-exclusion fence (Table 1; Figs 1, 2, 4, & 5). Presumably the cover of the alien grasses was unaffected by real or simulated grazing because of their strength as competitors. Interestingly, almost all the individual competitors removed in the weeding treatment of the field-compensation experiment were *Erodium cicutarium*, and it grew best without intraspecific competition. The ability to compete with *E. cicutarium* is probably an important reason that European grasses are dominant in California grasslands.

Timing of herbivory also influences plant response to herbivory (Crawley 1983; Maschinski & Whitham 1989; Strauss & Agrawal 1999). This should be particularly true for annual plants with short life spans, such as those in arid California valley grasslands. Crawley (1983) and Lennartsson et al. (1998) suggest that the early limit of the inductive period is fixed according to the amount of resources stored over winter in roots or seeds that are available for use early in the season, whereas the late limit is fixed by the degree to which meristems have not differentiated into reproductive material and can still be vegetative. *E. cicutarium* germinates and flowers early and continues to flower throughout the growing season, giving it a longer inductive time period than many later-maturing annual species (Bartolome 1979). Thus, the inductive time period for compensation and competitive abilities, along with the growth architecture, combine to determine the compensatory abilities and relative success of species in the California grassland community.

Conclusion

The removal of biomass through cattle grazing can create profound changes in grassland communities. Careful studies are necessary to document the responses of individual species and the entire community to grazing prior to the initiation of restoration attempts. At Carrizo Plain National Monument, cattle grazing harms many native plants, allowing non-natives and other strong competitors to proliferate. Investigation of the degree to which plants compensate following herbivory may be more

important than determining whether species exhibit under- or overcompensation. Alien species like *Erodium cicutarium* that only slightly undercompensate reproductively can still come to dominate a grazed community if native species are much more severely affected.

Acknowledgments

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