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Site-specific responses of native and exotic species to disturbances in a mesic grassland community

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Abstract. Grassland communities are increasingly recognized as disturbance-dependent ecosystems, yet there are few replicated, multi-site studies documenting vegetation responses to varying frequencies and types of grassland disturbance. Even so, land managers frequently manipulate disturbance regimes in an attempt to favour native grassland plants over exotic species. We conducted a factorial experiment testing three frequencies of clipping combined with litter accumulation, litter removal, and soil disturbance within the highly threatened California coastal prairie plant community. We monitored the response of native/exotic, grass/forb plant guilds once a year for four years. More frequent clipping reduced cover of exotic grasses and favoured exotic forbs, whereas native species were largely unaffected by clipping frequency. Litter accumulation, litter removal, and soil disturbance did not affect vegetation composition. Effects of litter accumulation may take longer than our experiment allowed, and soil disturbance due to our treatments was not sufficiently strong to show consistent effects relative to mammalian soil disturbance. Treatment response of some plant guilds differed among sites, highlighting the importance of replicating experiments at several sites before recommending conservation management practices.

Keywords: California; Clipping; Coastal prairie; Grassland restoration; Grazing; Litter accumulation; Litter removal; Mowing.

Abbreviation: UCSC = University of California, Santa Cruz.

Nomenclature: Hickman (1993).

Introduction

Common grassland disturbances, such as grazing and fire, simultaneously alter grasslands in a number of ways, yet the specific mechanisms by which these disturbances influence plant community composition are less well understood. For example, grazing reduces live vegetation (Grubb 1986; Belsky 1992; Mitchley & Willems 1995), while reducing litter (Sims et al. 1978; Knapp & Seastedt 1986; Menke 1992), disturbing the soil (Collins & Glenn 1988; McIntyre & Lavorel 1994), and redistributing nutrients (Steinauer & Collins 1995; Hobbs 1996). Past research suggests that litter reduction may increase safe sites for seedling recruitment (Harper 1977; Young & Evans 1989; Milchunas et al. 1992), but its differential effects on enhancing native vs. exotic species recruitment remains unclear. Other research suggests that soil disturbance associated with grazing may be more important than litter removal in influencing species composition (McIntyre & Lavorel 1994); soil disturbance may favour a number of rare native grassland herbs (Hobbs & Huenneke 1992; Kotanen 1995; McIntyre et al. 1995), as well as the invasion of exotic plant species (Hobbs & Atkins 1988; McIntyre & Lavorel 1994; Kotanen 1997). Understanding the relative importance of these different disturbance effects is essential as humans increasingly aim to conserve native species by managing ecosystems to mimic the disturbance regimes with which species have evolved.

There are few places where the effect of disturbance on grassland communities is more complex or controversial than in coastal California. Since the 1960s, conservationists have focused on purchasing remaining natural areas along California's coast and setting aside these lands as public parks. These parks contain the largest, most intact representations of California's grasslands and many rare, endemic species. In recent years, public land managers have increasingly removed cattle from these grasslands with little information about the impacts of cattle grazing or alternative disturbance regimes that might maintain rare species (Wilcove et al. 1998). Moreover, as California grasslands have become increasingly fragmented by development, cattle grazing has become logistically challenging. Therefore, some land managers are mowing small remnant grasslands to maintain a disturbance regime, although mowing may have different effects than grazing.

Past research has suggested the need to maintain the frequency and type of the disturbances with which grassland species have evolved (Axelrod 1985; Collins 1987; Davison & Kindscher 1999). Californian grasslands have evolved in response to unknown frequencies and intensities of ungulate and other large mammal disturbances (Axelrod 1985). These grasslands were widely impacted by Native American burning for at least 10 000 years and then by cattle grazing for nearly 250 years. For the past two centuries, these grasslands have also become increasingly dominated by exotic species introduced from other Mediterranean regions. This complicated disturbance history presents a conundrum for California's grassland managers, particularly because the prevalent exotic species may respond positively to disturbances such as cattle grazing (Painter 1995; Hayes & Holl 2003). Results of past studies, largely not replicated, have shown variable effects of grazing on both native and exotic plant species (Bartolome et al. 1986; Davis & Sherman 1992; Hatch et al. 1999).

Our previous research in coastal prairie suggests that exotic grasses, exotic forbs, and native annual forbs respond positively to cattle grazing; native grasses and native sedges are unaffected by grazing, and, native perennial forbs are negatively affected by grazing (Hayes & Holl 2003). This research, however, examined a broad suite of grazing regimes in paired grazed and ungrazed sites, but was unable to expressly address effects of varying disturbance frequency and type. We therefore conducted manipulative studies at three sites to test the effects of disturbance frequencies and certain disturbance mechanisms associated with cattle grazing on vegetation community composition, and to compare their effects with grazing. Specifically we tested the hypotheses that: (1) increased disturbance frequency would favour low-statured forbs, both native and exotic; (2) increased disturbance frequency would favour native grasses more than exotic grasses; and (3) removal of litter and increased bare ground would enhance establishment of native annual forbs and exotic species.

Methods

Study system

Traditionally, Californian grasslands have been differentiated into two major types, interior valley grasslands or coastal prairies, based on rainfall and temperature extremes. Interior valley grasslands are generally drier and hotter than coastal prairies. Coastal prairies are located below 1000 m a.s.l. within the moderating effects of the ocean (< 100 km from the coast) and are patchily distributed from southern Oregon to the Channel Islands of California (Heady et al. 1988). Characteristic native perennial grass species of coastal prairies include *Danthonia californica*, *Deschampsia caespitosa,* and *Nassella* spp. These grasslands are unique among Mediterranean grasslands in hosting a wide diversity of endemic annual and perennial forbs (Stromberg et al. 2002), which makes them of particular conservation concern.

Site description

We conducted research at three coastal prairie sites all within 4 km of the coast and at elevations of < 150 m a.s.l. The sites were each separated by 25 km along a largely north-south gradient in central California, near the city of Santa Cruz. In choosing research sites, areas had to meet the following criteria. All sites: (1) had been actively grazed by cattle until the beginning of study; (2) contained a relatively intact coastal prairie plant community; (3) had slopes of < 10% facing south to southeast; and (4) had sandy loam soils, deeper than 1 m. The final selection of sites depended on our ability to obtain permission both for regular and long-term access to the site and to establish experimental populations of a regulated, endangered plant species, the target of research discussed elsewhere. The names we use for the sites reflect place names from areas in close proximity: 'Elkhorn' (near the Elkhorn Slough, 36°52'4.3" N, 121°44'23.8" W), 'UCSC' (on the University of California Santa Cruz campus, 36°59' 5.5" N, 122°3'0.9" W), and 'Swanton' (near the town of Swanton, 37°4'13.4" N; 122°15'0.0" W). All sites have been grazed by cattle since at least the 1950s – but Swanton and UCSC were not grazed in the early 1990s . Elkhorn and UCSC were probably subjected to light tilling in the early 1900s.

Experimental design

At each of the three sites, we installed a single 52 m × 52 m fenced cattle exclosure in fall 1998 and initiated manipulative experiments within the exclosures in January 1999. We fenced the exclosures to exclude both cattle and feral pigs, as pigs increasingly cause disturbance in this region. Within each exclosure, we randomly allocated 30, 7 m × 7 m plots to ten treatments (described in detail below) with three replicates of each treatment. A 1-m buffer separated the plots and there was a 2-m buffer around the edge of the exclosure; we mowed the buffers every other month during the growing season.

The first level of treatments consisted of three vegetation clipping regimes using a motorized rotary trimmer to clip all vegetation to ca. 5 cm in height. The three vegetation clipping regimes were: (1) minimal clipping – vegetation clipped once in the spring (April) and once in the fall (September); (2) bimonthly clipping – clipping every other month through the growing season (January, March, May); and, (3) continual clipping – vegetation clipped once monthly through the growing season (January-June). We designed these disturbance regimes to provide a gradient of disturbance frequencies and to mimic common management regimes. The first regime (2 × per year treatment) was designed to constitute minimal disturbance. Such a regime would be the most practical alternative if cattle were removed from an area and their disturbance replaced by energy intensive, mechanical clipping. The second regime (3 × per year treatment) provided an intermediate level of disturbance, and mimics the increasingly common practice of 'rotational grazing' in which cattle are intensively grazed in an area for 3 to 5 d and rotated through areas at 45 to 60-d intervals (Voison 1959; Savory 1988). The final regime comprised a high level of disturbance (6 × per year treatment), simulating the historic cattle ranching practice of grazing throughout the growing season along the coast.

Each of the three clipping frequencies was subjected to a secondary set of treatments designed to test three types of cattle grazing related disturbances that have been shown to affect plant community composition: reducing live vegetation cover, litter removal, and soil disturbance. These treatments were: (1) clip and leave clipped material on the ground ('litter accumulation'); (2) clip and remove litter ('litter removal'); and, (3) clip, remove litter, and disturb the soil surface ('soil disturbance'). These treatments were performed sequentially as it was impossible to remove litter without clipping first, and to disturb soil without prior clipping and removal of litter. We removed litter with leaf rakes. For the soil disturbance treatment, we attached cow hooves to boots to simulate the combination of vertical and horizontal stresses of cow hooves (Scholefield & Hall 1986). A person took ten, high velocity steps/m^2. This resulted in disturbance of ca. 8% of the plots, which was typical for the stocking rate at the study sites (G. Hayes pers. obs.). The person applied ca. 80 kg of mass on each foot, which was characteristic of a small cow (Spedding 1971).

In addition to the nine frequency × secondary treatment combinations, we included a 'no disturbance' treatment where plots were neither clipped nor grazed throughout the study. Outside of the exclosure, in areas grazed by cattle, we marked three additional 7 m × 7 m plots adjacent to different sides of the exclosure. The grazed plots at the Swanton site were cleared of almost all vegetation by feral pigs between the 2000 and 2001 growing season; therefore, data from these plots are not presented. At Elkhorn, cattle grazed the plots at a stocking rate of 6 animals/ha for approximately 4 days at 45-60 day intervals from December through June each year, which is roughly equivalent to our 3×/yr treatment. At UCSC, cattle grazed the site continuously during the months of March and May at a lower stocking rate of 3 animals/ha.

Abiotic variables

We compiled rainfall and temperature data from the nearest meteorological station managed by the California Department of Water Resources. Stations were located at similar elevations within 4 km of each research site. We took ten litter depth measurements at 40-cm intervals along a diagonal of each plot in June 2002 (year 4 of the treatments).

In September 1999, we collected baseline soil nutrient data by gathering 25, 2.5-cm diameter × 10-cm depth soil cores from evenly spaced intervals throughout each site. These samples were bulked and then analysed for pH, cation exchange capacity, organic matter, texture, total Kjeldahl nitrogen, and exchangeable phosphorus, potassium, calcium, and magnesium. The soils were analysed using standard methods (Anon. 2002) at the University of California, Davis' Division of Agriculture and Natural Resources Analytical Laboratory.

Vegetation data

In each plot, we monitored the plant community cover in late-March/early-April of each year from 1999 to 2002 using the point-intercept method (Mueller-Dombois & Ellenberg 1974). We placed four grids at permanent locations in the centre of each plot; the centres of the plots were not disturbed by other experiments, such as phytomass data collection (not described here). We recorded each species only once at each sample point if it intersected a 1.5 mm metal pin lowered at intersections of strings spread across a 0.5 m × 0.5 m grid at 10 cm intervals (a total of 25 points). We identified species and their origin (native or exotic) using The Jepson Manual (Hickman 1993).

Statistical analysis

All analyses were done using SAS version 8.01. We were most interested in the cover of plant guilds relative to one another in response to treatments. Therefore, we used relative cover data (number of intercepts of focal species/total number of vegetation intercepts) in our analyses as the total number of vegetation-pin intercepts varied by treatment in some years, largely due to how recently specific treatments had been clipped before sampling. We initially analysed vegetation community data (except grazed treatments, for which we had data only at two sites) using univariate repeated measures ANOVA with site and experimental treatments as fixed factors, sampling year as the repeated factor, and the relative cover of the following three guilds of plants as response variables: exotic grasses, exotic forbs, and native grasses.

We used the Huynh-Feldt adjustment when the assumption of sphericity was not met (Von Ende 1993). Initially, repeated measures analyses of guild cover through time showed strong site × time and site × treatment interactions. Therefore, we report separate analyses for each site and year following the initial year (1999) when composition showed little difference between treatments. When litter removal and soil disturbances did not show effects (the vast majority of cases), we pooled the data from these secondary treatments and focused on clipping frequency. We used Tukey's LSD mean comparison procedures to separate specific treatment effects when treatment was significant in the ANOVA with a significance level of $P < 0.05$. Percentage values were arcsine transformed when necessary to meet assumptions of normality and homogeneity of variances.

Results

Abiotic factors

During the four years of our research, annual rainfall ranged from 290 to 840 mm; the Elkhorn site received the least rainfall (358 ± 104 mm), UCSC was intermediate (756 ± 99 mm), and the Swanton site received the most rainfall (916 ± 183 mm). Seasonal rainfall was close to average in 1999, 2000, and 2002 (except at Elkhorn) and below the 20-yr average in 2001 (and 2002 at Elkhorn). Mean rainy season temperature for the sites was 12.1 °C and mean dry season temperature was 16.4 °C. Soils at all sites were sandy loams with minor variations in pH (5.0 ± 0.3), organic matter (2.0 ± 0.3%), and major nutrients (12.2 ± 2.5 meq/100g CEC; 0.4 ± 0.1 meq/100g X-K; 4.9 ± 1.4 meq/100g X-Ca; 1.5 ± 0.2 meq/100g X-Mg; 6.4 ± 4.9 ppm P). The Elkhorn site had a higher sand content (Elkhorn: 68%; Swanton: 56%; UCSC: 43%) and a lower silt content (Elkhorn: 20%; Swanton; 32%; UCSC: 35%) whereas the UCSC site had a slightly higher clay content (Elkhorn & Swanton: 12%; UCSC: 22%).

In June 2002, after four years of treatments, the no disturbance plots had substantially thicker litter at all sites, and the litter accumulation and grazed treatments generally had slightly higher litter levels than litter removal plots (Fig. 1). Litter depths were greater at the Elkhorn and Swanton sites. Our soil disturbance treatments had no consistent effect on the amount of bare soil in any of the years of the study, because there was high variance within treatments due to small mammal burrowing activity (Fig. 2, data shown from 2002 only).

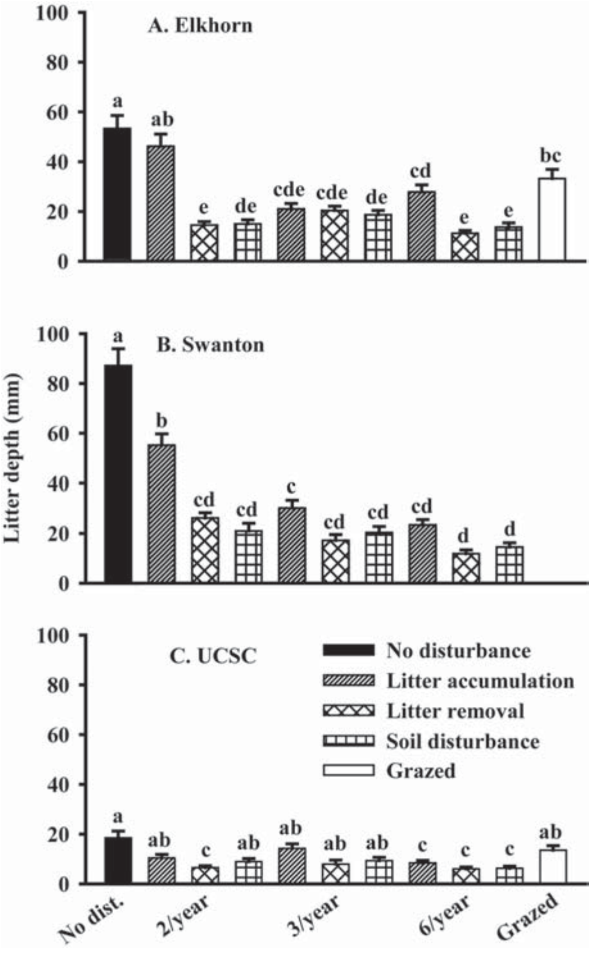

Fig. 1. Litter depth at the three study sites in June 2002 ($n = 3$). Error bars indicate 1 *SE*. Means with the same letter are not significantly different ($P < 0.05$) based on Tukey's LSD.

Vegetation effects

Surprisingly, secondary disturbances (litter removal and soil disturbance) did not affect the vegetation community composition in the four years of the survey, so we report the effects of clipping frequency using pooled data from these secondary treatments.

European plant species, especially annual grasses, had consistently more cover across all three sites at the outset of the experiment; this is characteristic of California grasslands, even those with comparatively high proportions of native species. The most common species at all three research sites included the exotic annual grass species *Bromus* and *Hordeum* spp., *Lolium multiflorum*, and *Vulpia bromoides* (Table 1). At the Elkhorn and Swanton sites, exotic grass cover was lower in the more frequently clipped plots after the first year (Fig. 3). At the UCSC site this trend was much weaker in 2001 and not observed in the other years; the difference at the UCSC site results from the invasion of *Brachypodium distachyon*, a low-statured grass which increased in cover from no detected cover in 1999 to 30.9 ± 2.0% cover in 2002. At Elkhorn, exotic grass cover in the grazed plots was similar to the 2×/yr treatment.

The dominant forb species were different at all sites in 1999 (Table 1). *Plantago lanceolata* was the only species common to all sites and was particularly abundant at the UCSC site. *Erodium* spp. and *Trifolium subterraneum* had high cover at the Swanton site in all years (Table 1), and increased in cover in clipped and grazed plots during the study at Elkhorn and UCSC (*Erodium* spp. only). Generally, exotic forb cover was higher in more frequently clipped and grazed plots (Fig. 4); this trend was less pronounced at UCSC, likely reflecting differences in species composition.

The Elkhorn site had the most native grass cover, primarily *Danthonia californica* (Table 1). Both the Swanton and UCSC sites had low native grass cover comprised of *Bromus carinatus* (Swanton only), *Danthonia californica* and *Nassella pulchra*. There were no statistically significant treatment effects in any year for this guild (Fig. 5).

The native sedge guild was the least abundant at our research sites although it is notably prevalent in many California coastal prairie areas (Hayes & Holl 2003). Sedges, including *Juncus occidentalis*, *J. phaeocephalus* and *Scirpus koilolepis,* were found primarily at the Elkhorn site (Table 1). The native forb guild was not abundant in any year and varied strongly among sites in the baseline year, 1999 (Table 1). The main native forb species at the Elkhorn site was the late-season annual *Madia sativa* along with some scattered plants of *Oenothera ovata*.

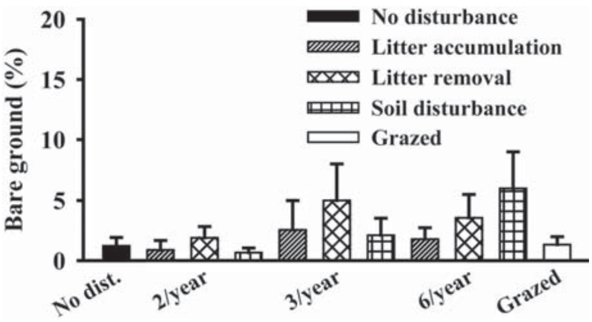

Fig. 2. Bare ground averaged across the three study sites in March 2002 (n = 3). Error bars indicate 1 *SE*. No means differed significantly ($P < 0.05$) based on Tukey's LSD.

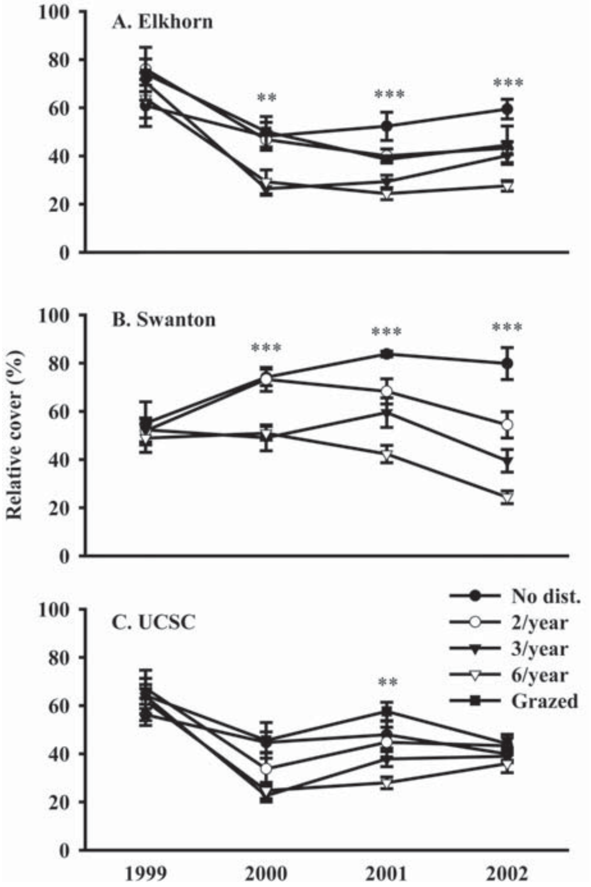

Fig. 3. Relative percent cover of exotic grasses over time at the three study sites. Error bars indicate 1 *SE*; n = 3 for no disturbance and grazed plots, n = 9 for other treatments. ** = $p < 0.01$; *** = $p < 0.001$ based on ANOVA.

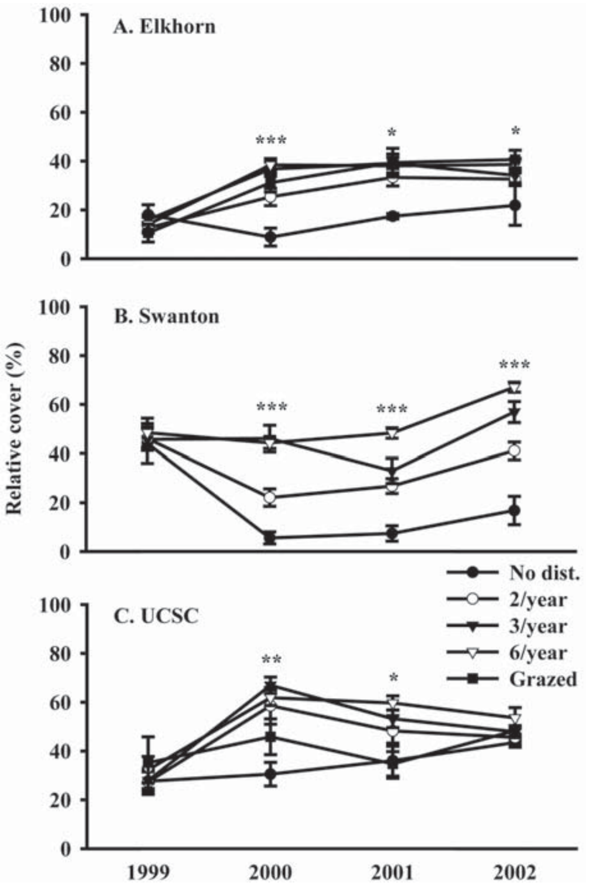

Fig. 4. Relative percent cover of exotic forbs over time at the three study sites. Error bars indicate 1 *SE*; *n* = 3 for no disturbance and grazed plots; *n* = 9 for other treatments. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$ based on ANOVA.

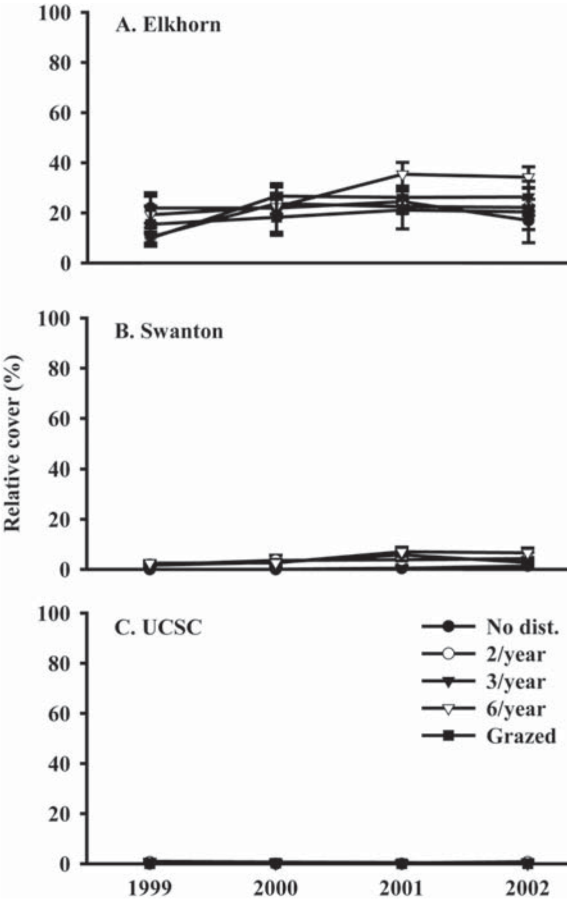

Fig. 5. Relative percent cover of native grasses over time at the three study sites. Error bars indicate 1 *SE*; *n* = 3 for no disturbance and grazed plots; *n* = 9 for other treatments. No significant differences based ANOVA.

At the UCSC site, the most abundant was *Eschscholzia californica,* which is a short-lived perennial at this site. *E. californica* had significantly higher cover in no disturbance plots at UCSC in the first two years of the study (1999: $F = 3.2$; $P = 0.0355$; 2000: $F = 4.2$; $P = 0.0147$), but was not significantly affected by treatments thereafter (2001: $F = 2.2$, $P = 0.1400$; 2002: $F = 1.0$; $P = 0.4195$). The cover of all other sedges and native forbs was sufficiently low that we could not perform statistical comparisons on these guilds.

Discussion

Four important points arise from the results of this research. First, our research shows that grazing or clipping favour exotic forbs over exotic grasses, rather than shifting the balance between exotic and native species, as expected. This result concurs with a substantive literature suggesting a decrease in grasses and an increase in forbs with increasing disturbance (Dyksterhuis & Schmutz 1947; Branson & Weaver 1953; Collins & Glenn 1988; Ash & McIvor 1998; Fensham et al. 1999; Bullock et al. 2001). Decreased canopy height and damage to higher-statured species are likely driving factors in this shift. In our system, exotic grasses invest a large percentage of phytomass above ground, and are more vulnerable to clipping, favouring shorter-statured exotic forbs (Noy-Meir et al. 1989; Noy-Meir 1993; McIntyre et al. 1995) that may take advantage of reduced light competition in clipped or grazed plots.

Table 1. Relative percent cover of the plant guilds and the major species representing each plant guild at each site in 1999. Values are means ± 1 *SE*. Letters in parentheses indicate A = annual, P = perennial.

Guild/Major species	Elkhorn	Swanton	UCSC
Exotic grasses	69.3 ± 3.1	51.4 ± 2.8	63.4 ± 2.5
Vulpia bromoides (A)	40.1 ± 2.9	8.5 ± 1.6	41.2 ± 2.0
Bromus and *Hordeum* spp. (A)	10.0 ± 1.7	21.9 ± 2.1	18.3 ± 1.4
Lolium multiflorum (A)	18.7 ± 2.0	21.2 ± 1.7	5.0 ± 1.0
Exotic forbs	14.6 ± 1.3	46.5 ± 2.6	29.0 ± 2.5
Erodium spp. (A)	0.9 ± 0.3	14.5 ± 1.7	2.7 ± 0.4
Geranium dissectum (A)	3.1 ± 0.4	1.0 ± 0.2	2.0 ± 0.5
Hypochaeris radicata (P)	1.5 ± 0.4	8.2 ± 1.1	0.1 ± 0.1
Plantago lanceolata (P)	4.5 ± 0.7	5.4 ± 1.1	22.0 ± 2.4
Trifolium dubium (A)	1.9 ± 0.4	0.6 ± 0.2	0
Trifolium subterraneum (A)	1.3 ± 0.3	10.5 ± 1.3	0
Native grasses	9.0 ± 1.3	1.7 ± 0.5	0.5 ± 0.3
Danthonia californica (P)	8.6 ± 1.4	0.6 ± 0.3	0
Nassella pulchra (P)	0.3 ± 0.3	0.2 ± 0.1	0.2 ± 0.2
Bromus carinatus (P)	0	0.9 ± 0.4	0.3 ± 0.3
Native forbs	2.2 ± 0.5	0.3 ± 0.1	5.4 ± 1.1
Calandrinia ciliata (A)	0	0.3 ± 0.1	0
Eschscholzia californica (P)	0	0.1 ± 0.1	6.2 ± 1.4
Madia sativa (A)	2.0 ± 0.6	0	0
Native sedge	1.6 ± 0.8	0.01 ±0.01	0

Second, as Foin & Hektner (1986) did, we recorded no effect of removing grazing on any native plant guild, with the exception in our study of the native forb *Eschscholzia californica,* which showed only a short-term growth effect when released from disturbance at one site. In contrast, other studies have found that release from grazing resulted in lower cover of *Danthonia californica* (Hatch et al. 1999; Hayes & Holl 2003), the dominant native grass in this study, and native annual forbs (Hayes & Holl 2003), perhaps because grazing reduces exotic grass cover and plant litter (Bartolome & Gemmill 1981; Fossum 1990). It is likely that seed dispersal may be a limiting factor for the establishment of native grassland species (Coulson et al. 2001; Bischoff 2002), particularly in our study, given the low cover of native grasses, sedges, and forbs regardless of disturbance regime. Most native California coastal prairie species show no apparent long-distance dispersal mechanisms, except possibly movement by mammals, which is limited by the high degree of habitat fragmentation. Grassland restoration may require reintroduction of species in addition to maintenance of appropriate disturbance regimes. It is also possible that we did not record the full complement of native species present in the seed bank during the four years of our experiment. Seedling establishment from dormant seedbanks in Mediterranean climates is notoriously episodic (Hobbs & Mooney 1991) and the period of our study did not include years with particularly high rainfall.

It is difficult to compare the relative effects of grazing and clipping on community composition from our study since the grazing regimes varied at the two sites for which we have data. At Elkhorn, community composition was similar in grazed and 2×/yr plots, although the grazing frequency at Elkhorn was more similar to the 3×/yr clipping treatment. At UCSC, where grazing started later in the year and was less intense, the grazed plots differed only from the most frequently clipped plots. It is clear from our work that our clipping regime more strongly affected community composition than grazing, when both are compared to no disturbance. This result is not surprising since we clipped and raked uniformly, whereas cows graze and defecate patchily resulting in some areas as short as our clipped plots and others that are taller due to fertilization and less vegetation removal (Steinauer & Collins 1995; Hobbs 1996). Further sampling of the more heterogeneous grazed pastures was needed to make stronger comparisons between grazing and clipping.

A third, surprising result of our work is that the secondary disturbances of litter accumulation, litter removal, and soil disturbance did not affect the cover of any guild during the 4-yr period of this study. This contradicts the hypothesis that litter accumulation drives grassland community composition (Facelli et al. 1988), but confirms the hypothesis that canopy height is more important than litter accumulation in mesic grasslands (Monk & Gabrielson 1985; Grubb 1986; Belsky 1992;

Mitchley & Willems 1995). The fact that our litter accumulation treatments succeeded in increasing litter depth but did not affect vegetation community composition, suggests that canopy height may be more important than litter in our system. Litter decomposition measurements in Californian grasslands indicate accumulation periods of several years (Heady et al. 1988), and changes in community composition may only begin after maximum accumulation of litter, suggesting that litter effects might emerge over a longer period of time.

We had hypothesized that our soil disturbance treatment would provide safe sites for seedlings (McIntyre et al. 1995; Kiviniemi & Eriksson 1999), especially native annual forbs (Hobbs et al. 1988; Meyer & Schiffman 1999) and exotic species (Hobbs & Atkins 1988; D'Antonio 1993; McIntyre & Lavorel 1994). Our soil disturbance treatment slightly increased bare soil, but within-treatment variation was high due to soil disturbance by small mammals. We conclude that only in heavily grazed sites will trampling increase bare ground relative to other mammalian soil disturbance, but we are unable to assess the importance of bare areas as safe sites for certain plant guilds.

The final, and arguably most important point stemming from our research is that it is essential to replicate studies at multiple sites when drawing general conclusions and management recommendations. Many wide-ranging conclusions on the importance of disturbance to grassland community composition and productivity have been drawn based on manipulative studies conducted at single sites (e.g., Hobbs & Mooney 1991; Wilson & Tilman 1991; Burke & Grime 1996; Shaw et al. 2002), despite the recognized risk of extrapolating results beyond the spatial extent from which samples were selected (Hurlburt 1984). Our results corroborate this risk. Although some trends were similar in all three of our research sites, responses frequently varied, even though we selected sites that were relatively similar with respect to soil, slope, aspect, and initial vegetation. For example, if we had drawn conclusions regarding the effects of clipping on exotic grasses from manipulations at the UCSC site alone, our conclusion would have been quite different (minimal effects) compared to at the other two sites (clipping strongly reduced exotic grass cover). We realize that replicating experiments is costly and time consuming, but reiterate that it is essential to make credible statements about the disturbance effects in different ecosystem types and to provide useful recommendations to land managers.

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