

The roles of exotic grasses and forbs when restoring native species to highly invaded southern California annual grassland

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Abstract Many semi-arid shrublands in the western US have experienced invasion by a suite of exotic grasses and forbs that have altered community structure and function. The effect of the exotic grasses in this area has been studied, but little is known about how exotic forbs influence the plant community. A 3-year experiment in southern California coastal sage scrub (CSS) now dominated by exotic grasses was done to investigate the influence of both exotic grasses (mainly *Bromus* spp.) and exotic forbs (mainly *Erodium* spp.) on a restoration seeding (9 species, including grasses, forbs, and shrubs). Experimental plots were weeded to remove one, both, or neither group of exotic species and seeded at a high rate with a mix of native species. Abundance of all species varied with precipitation levels, but seeded species established best when both groups of exotic species were removed. The removal of exotic grasses resulted in an increase in exotic and native forb cover, while removal of exotic forbs led to an increase in exotic grass cover and, at least in one

year, a decrease in native forb cover. In former CSS now converted to exotic annual grassland, a competitive hierarchy between exotic grasses and forbs may prevent native forbs from more fully occupying the habitat when either group of exotics is removed. This apparent competitive hierarchy may interact with yearly variation in precipitation levels to limit restoration seedings of CSS/exotic grassland communities. Therefore, management of CSS and exotic grassland in southern California and similar areas must consider control of both exotic grasses and forbs when restoration is attempted.

Keywords *Bromus* · California annual grassland · Coastal sage scrub · *Erodium* · Grassland restoration · Removal experiment

Introduction

Since European contact, arid and semi-arid shrub communities in western north America have been extensively invaded by exotic grasses (Mack 1981; Laycock 1991; Allen et al. 1998; Minnich and Dezzani 1998; DiTomaso 2000). These exotic grasses compete against native shrubs and herbaceous plants (Schultz et al. 1955; Litav et al. 1963; Bush and Van Auken 1989), changing the species composition of the native communities they invade (D’Antonio and Vitousek 1992; Mack and D’Antonio 1998). In many

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cases, these invasions have formed novel communities that resist both natural succession and deliberate restoration back to a pre-invasion state (Mack 1981; Stylinski and Allen 1999; Allen et al. 2005).

Exotic forbs have also invaded many of the same areas, although their effect on invaded communities is less well understood. This is in part because some invasions occurred long before native communities had been assessed, and even before dominant exotic grasses had invaded. For example, exotic species of *Erodium* may have become naturalized in California by 1769 (Hendry and Kelly 1925; Hendry 1931; Mensing and Byrne 1998; Minnich 2008), and have since invaded wide areas of the western United States. Consequently, there is little information about how these exotic forbs influence the management, conservation, or restoration of semi-arid shrublands.

In southern California, coastal sage scrub (CSS) is a highly diverse, semi-arid shrub community that has been invaded by both exotic grasses and exotic forbs (Westman 1981; Mensing and Byrne 1998; Bowler 2000). Although it is difficult to estimate the area originally occupied by CSS, there is general agreement that it is currently much reduced from its former extent, and that what little is left is often highly disturbed and altered from its pre-disturbance structure and composition by inclusion of these non-native grasses and forbs (Westman 1981; Minnich and Dezzani 1998; Bowler 2000). Like many other semi-arid shrub communities, CSS has been transformed over much of its range into self-perpetuating communities dominated by annual grasses (especially *Bromus* spp.) of Mediterranean origin (Mack 1981; Laycock 1991; Allen et al. 1998; Minnich and Dezzani 1998). Also in common with other semi-arid shrub communities, current and former CSS areas are often invaded to a significant degree by exotic forbs, including species of *Erodium*. The influence of exotic grasses on the structure and function of native communities, including CSS, has been extensively studied (Mack and D'Antonio 1998; D'Antonio and Vitousek 1992; Eliason and Allen 1997), and restoration attempts have shown that the native species can be very sensitive to even low cover of exotic grasses (i.e. even 25 grasses m⁻², Eliason and Allen 1997). However, it is not clear how the exotic forbs interact with the grasses in these competitive relationships (Gillespie and Allen 2004, 2008; Allen et al. 2005).

In situ plant removal studies can be useful for demonstrating competitive roles in plant communities (Diaz et al. 2003). Such studies have shown non-reciprocal responses by remaining species (Allen and Forman 1976) such that the removal of one species may cause a suite of species responses that are entirely different than those caused by the removal of another species. Such unique interspecific interactions may play a significant role in development, coexistence, and maintenance of diversity in plant communities (Chesson 2000), and may have implications for restoration and other management activities. Previous work (Brooks 2000; Allen et al. 2005; Cox and Allen 2008) has suggested that exotic forbs may limit restoration success when exotic grasses are controlled in CSS areas. We conducted a removal experiment to further investigate the relationship between exotic grasses, exotic forbs, and native species, and how they interact in former CSS areas now dominated by exotic grassland in southern California. We hypothesized that exotic grasses and forbs would interact to limit the native species in this system. Understanding these interactions will help land managers, restoration practitioners, and scientists to more effectively manage and restore this plant community for native species.

Methods

Study site and experimental design

The Shipley reserve (33°39'18"N, 116°59'49"W), where the study was conducted, was established as part of the western Riverside County multi-species habitat reserve, California, in 1992 to provide habitat connectivity between two reservoirs. The reserve includes several vegetation types, including oak-woodland, chaparral, CSS, and annual grassland. Precipitation in the region over the last 19 years was ca. 250 mm per year, occurring almost exclusively during the winter/spring growing season of November–April. Precipitation during the years of this study varied greatly, with the 1st July–30th June water year of 2002–2003 receiving roughly average precipitation (280 mm), 2003–2004 receiving below average precipitation (176 mm), and the final year of the study, 2004–2005, receiving precipitation above the average (449 mm). Although the early history of the reserve

is not well documented, valley bottoms were likely disked and cleared of native vegetation (including CSS) during the late 1800's to early 1900's. The ensuing cultivation of these areas resulted in the current situation of plant communities dominated by exotic annual grasses and forbs, with little or no cover of native shrubs (Allen et al. 2005). Native forbs remain, though apparently much reduced (Minnich 2008) and generally overtopped by the abundant exotic grasses.

To investigate how exotic species influence native species cover and the potential for restoration of native plants, a removal experiment was established in 2003 and repeated in 2004 as a $2 \times 2 \times 2$ factorial design replicated in 10 blocks and repeated in each of 2 years, for a total of 80 plots each year and 160 plots overall. Plots measured 0.5×1.0 m. Treatment factors were: exotic grass removal (removed or left in place), exotic forb removal (removed or left in place), seeding (seed added or not added), and year of establishment (2003 or 2004). Treatments were fully crossed and randomly assigned within each block. Plots were weeded only once, after germination commenced following rains in the first winter growing season. Weeding occurred from 7 to 13th January 2003 for plots established in the 2003 growing season, and from 10 to 16th December 2003 for plots established in the 2004 growing season. Plants were hand-pulled as seedlings to minimize soil disturbance. A 10 cm buffer, corresponding to the treatment, was also weeded around each plot.

Plots were seeded after weeding was finished. Plots established during the 2003 growing season

were seeded with native species on 7th February 2003, and plots established during the 2004 growing season were seeded on 1st January 2004. In both years, precipitation was at least 80 mm after seeding (February 2003 precipitation = 102.1 mm, February 2004 precipitation = 84.8 mm, data from California Irrigation Management Information System [CIMIS] weather station, Riverside, County, California, USA, <http://www.cimis.water.ca.gov>, accessed May 2006). Seeds were mixed before seeding and broadcast by hand. Native species were selected for seeding based on their presence in the area and on availability of seed. Both forbs and shrubs were included in the mix to represent the native community at the site and to give an indication of how the different classes of exotic species limit the native community. Species were seeded at a relatively high rate (based on our prior experience at this site) in order to provide ample germinants for analysis. Native seeds collected from local populations were donated by a commercial seed company (S&S Seeds, Carpinteria CA). Species seeded and their respective seeding rates (in viable seed per m^2) are listed in Table 1.

Data and analysis

Each plot was observed for two growing seasons (i.e. plots established in the 2003 growing season were observed through 2004, and plots established in the 2004 growing season were observed through 2005). Data were collected in late spring each year from 2003 to 2005, and included percent aerial cover (by visual estimation to the nearest percent in gridded

Table 1 Native species and numbers seeded, in viable seeds per m^2

Species	Lifespan	Growth form	Seeding rate (seeds/ m^2)
<i>Artemisia californica</i>	Perennial	shrub	122
<i>Castilleja exserta</i>	Annual	forb	204
<i>Eriogonum fasciculatum foliosum</i>	Perennial	shrub	95
<i>Gutierrezia californica</i>	Perennial	shrub	15
<i>Lasthenia californica</i>	Annual	forb	167
<i>L. filaginifolia</i> (not seeded in 2004)	Perennial	forb	1
<i>L. bicolor</i>	Annual	forb	7
<i>L. sparsiflorus</i> (not seeded in 2004)	Annual	forb	14
<i>Salvia apiana</i>	Perennial	shrub	42

Lessingia filaginifolia and *Lupinus sparsiflorus* were seeded only in 2003, as seeds were not available in 2004. Seeds were donated by S&S Seed Co., Carpinteria, CA. Nomenclature follows Hickman (1993)

frames) of all species and the number of individuals of seeded species that had emerged in each plot and survived until the late spring survey. As in other studies of CSS (Gillespie and Allen 2004; Allen et al. 2005) and of biodiversity functional analysis (Suding et al. 2005), species were grouped (exotic grasses, exotic forbs, unseeded native forbs and shrubs, and seeded forbs and shrubs) for analysis because many species are too infrequent to analyze separately. The 11 taxa present in at least 20% of the 160 plots (exotic grasses: *Avena barbata*, *Bromus diandrus*, *Bromus hordeaceus*, *Bromus madritensis* subsp. *rubens*, *Hordeum murinum*; exotic forbs: *Erodium brachycarpum*, *E. cicutarium*; native forbs: *Amsinckia menziesii*, *Eremocarpus setigerus*, *Lupinus bicolor*, *Trifolium* spp.) were also examined separately to assess the degree to which species response patterns were consistent with grouped results.

Because the experiment was repeated for 2 years and each plot was observed for two seasons, matching growing seasons from each year's plots were analyzed together, e.g. data from the first season of plots established in 2003 and the first season of plots established in 2004 were analyzed to test the effect of year of establishment, seeding treatment, removal of exotic grasses, and removal of exotic forbs on the dependent variables (cover of exotic grass, exotic forb, native forb, and seeded species). Likewise, data from the second season of each plot were analyzed separately from the first growing season. Cover data were arcsine transformed, seedling data were square-root transformed, and both were analyzed with SAS (SAS Institute 2006) using mixed models analysis to test the fixed effects of removal treatments, seeding, and year of establishment on the cover or density of each species group. Block effects were nested within their seeding year, and designated as random effects in the analyses. Post-hoc mean separations were performed with the Tukey HSD test, which controls *P*-values for multiple comparisons (SAS Institute 2006).

Results

During the experiment, we observed 19 exotic and 38 native species (Tables 2 and 3, respectively). Individual species examined displayed similar patterns to their analysis groups. Precipitation likely exerted a

strong influence over the vegetation during the years of this study. For example, in plots where exotic forbs were removed, cover of native forbs during the dry 2004 growing season averaged less than 5%, compared to 20% during the 2003 season, when precipitation levels were approximately average (Fig. 3a).

As expected, weeding reduced cover of the weeded groups, and often increased the cover of the non-weeded groups. Exotic forb removal in season one increased cover of exotic grasses if grasses were not also weeded (Interaction $F_{1,126} = 11.9$, $P = 0.0008$) (Fig. 1). Season two plots that experienced grass removal the previous season also had lower grass cover than plots where exotic grasses were not removed (grass removal main effect: $F_{1,126} = 30.4$, $P < 0.0001$) (data not shown). Similarly, exotic forb cover in season one was lower in both years in plots from which exotic forbs had been removed (forb removal main effect: $F_{1,126} = 31.9$, $P < 0.0001$)

Table 2 Non-native species and frequency (160%, 1 × 0.5 m plots they occupied) over two growing seasons in experimental plots established in 2003 and 2004

Family	Species	Frequency
Exotic grasses		
Poaceae	<i>B. madritensis</i> subsp. <i>rubens</i>	52
	<i>B. hordeaceus</i>	51
	<i>B. diandrus</i>	48
	<i>A. barbata</i>	22
	<i>H. murinum</i>	21
	<i>Vulpia myuros</i>	16
	*1 infrequent species	
Exotic forbs		
Geraniaceae	<i>E. brachycarpum</i>	58
	<i>Erodium cicutarium</i>	23
Brassicaceae	<i>Hirschfeldia incana</i>	13
	<i>Sisymbrium irio</i>	10
Asteraceae	<i>Filago gallica</i>	6
	<i>Hypochaeris glabra</i>	6
	*6 infrequent species	

Species are listed in order of observed frequency. Nomenclature follows Hickman (1993)

* Infrequent species (present in <5% of plots): exotic grass = *Schismus barbatus* (Poaceae), exotic forbs = *Silene gallica* (Caryophyllaceae), *Centaurea melitensis* (Asteraceae), *Cnicus benedictus* (Asteraceae), *Lactuca serriola* (Asteraceae), *Anagallis arvensis* (Primulaceae), *Amaranthus albus* (Amaranthaceae)

Table 3 Native species and frequency (160%, 1 × 0.5 m plots they occupied) over two growing seasons in experimental plots established in 2003 and 2004

Family	Species	Frequency
Native forbs		
Euphorbiaceae	<i>Eremocarpus setigerus</i>	48
Fabaceae	<i>L. bicolor</i>	41
Boraginaceae	<i>Amsinckia menziesii</i>	36
Fabaceae	<i>Trifolium spp.</i>	32
Asteraceae	<i>L. californica</i>	16
Asteraceae	<i>Hemizonia kelloggii</i>	12
Onagraceae	<i>Clarkia purpurea</i>	11
Asteraceae	<i>Stephanomeria exigua</i>	9
Fabaceae	<i>Lotus hamatus</i>	6
Onagraceae	<i>Camissonia bistorta</i>	6
Violaceae	<i>Viola pedunculata</i>	6
	*23 infrequent species	
Native Shrubs		
Lamiaceae	<i>Salvia mellifera</i>	9
	*3 infrequent species	

Species are listed in order of observed frequency. Nomenclature follows Hickman (1993)

* Infrequent species (present in <5% of plots): native forbs = *Calandrinia ciliata* (Portulacaceae), *Castilleja exserta* (Scrophulariaceae), *Centaurium venustum* (Gentianaceae), *Chamaesyce albomarginata* (Euphorbiaceae), *Conyza canadensis* (Asteraceae), *Cryptantha intermedia* (Boraginaceae), *Daucus pusillus* (Apiaceae), *Emmenanthe penduliflora* (Hydrophyllaceae), *Eriastrum saphirinum* (Polemoniaceae), *Juncus bufonius* (Juncaceae), *Lessingia filaginifolia* (Asteraceae), *Linaria canadensis* (Scrophulariaceae), *Loeflingia squarrosa* (Caryophyllaceae), *Lotus* spp. (Fabaceae), *Lotus strigosus* (Fabaceae), *L. sparsiflorus* (Fabaceae), *Mimulus guttatus* (Scrophulariaceae), *Navarretia atractylodes* (Polemoniaceae), *Plagiobothrys* spp (Boraginaceae), *Platystemon californicus* (Papaveraceae), *Trichostema lanceolatum* (Lamiaceae), *Uropappus lindleyi* (Asteraceae), 13 plots had an unidentified species, native shrubs = *A. californica* (Asteraceae), *Eriogonum fasciculatum* (Polygonaceae), *S. apiana* (Lamiaceae)

(Fig. 2a), and higher in both seasons in plots from which exotic grasses had been removed (season one grass removal main effect: $F_{1,126} = 17.2$, $P < 0.0001$, season two grass removal main effect: $F_{1,126} = 23.3$, $P < 0.0001$) (Fig. 2b).

Year of establishment and weeding treatments influenced cover of native forbs during season one. Exotic forb removal significantly reduced native forb cover in 2003 but not in 2004 (which was a dry year), resulting in a significant interaction term (interaction

$F_{1,126} = 8.4$, $P = 0.004$) (Fig. 3a). Plots established in January 2004, when precipitation was low, displayed uniformly low cover of native species (Fig. 3a). In both seasons, plots from which exotic grasses were removed had slightly higher cover of native forbs than plots in which grasses remained (season one grass removal main effect: $F_{1,126} = 14.7$, $P = 0.0002$; season two grass removal main effect: $F_{1,126} = 12.8$, $P = 0.0005$) (Fig. 3b).

In plots where seed was added, an interaction of exotic grass removal by exotic forb removal was significant in season one, so that plots that experienced removal of both exotic grasses and exotic forbs had higher density of seeded forbs compared to plots where exotic grasses were present (interaction: $F_{1,126} = 4.0$, $P = 0.047$) (Fig. 4). Season two results were similar, but without the interaction: seeded forbs had highest density in plots where exotic grasses or forbs were removed (grass removal main effect: $F_{1,126} = 12.1$, $P = 0.0007$; forb removal main effect: $F_{1,126} = 19.6$, $P = 0.0001$) (data not shown).

Discussion

The outcome of restoration and management efforts in former CSS areas now dominated by exotic annual grasses may depend on complex relationships between the different functional groups of exotic and native species and the variable precipitation of the region. We found evidence that in a year of average precipitation (2002–2003), an apparent competitive hierarchy occurs between exotic grasses and forbs such that if exotic grasses are removed, exotic forbs expand and prevent native forbs from fully occupying the vacant habitat, and that if exotic forbs are removed, exotic grasses increase and exclude native forbs (Figs. 2, 4a). In dry years, however, we found that these strong species interactions may be limited by low productivity (measured as percent cover) of both exotic and native species. We also found that under these limitations, seeding native species is not effective at substantially increasing native species cover, although density of seeded species may increase when all exotic species are removed (Fig. 4).

Although care should be taken when inferring competitive relationships on the basis of removal experiments (Dormann and Brooker 2002; Diaz et al.

2003), they are useful for elucidating the influence of the removed species on their plant communities (Allen and Forman 1976; Wardle et al. 1999; Lyons and Schwartz 2001; Symstad and Tilman 2001; Dormann and Brooker 2002; Jurjavcic et al. 2002; Lenz et al. 2003). Because exotic grasses contribute most to the overall biomass and cover at these locations, plots that experienced removal of exotic grasses also experienced a greater removal of biomass than forb removal plots, and might lead one to expect large increases in cover of native species. However, because exotic forbs also responded to grass removal, native forbs were unable to increase significantly. Furthermore, in a year of average precipitation, the dominant exotic grasses increased at the expense of native forbs when exotic forbs were removed from the community (Figs. 1, 3a, plots established in 2003). This closing of the exotic grassland community suggests that removal of exotic forbs could increase the dominance of exotic grasses, resulting in even lower abundance of native forbs in these communities, similar to an extinction cascade where loss of one species precipitates further species losses (Lundberg et al. 2000).

Year-to-year variation in precipitation has also been known to exert a strong influence on the annual species in these communities (Keeley et al. 2005). In fact, the influence of precipitation on our data was evident, since plots that were established during the average precipitation year of 2002–2003 had up to 34% cover of native forbs during the first growing

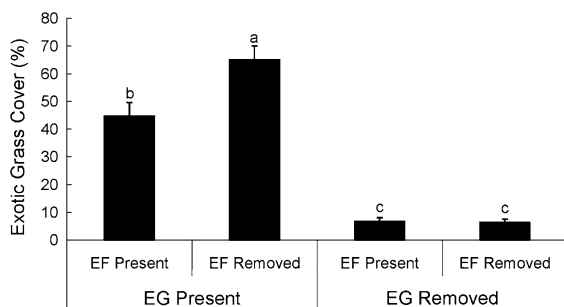


Fig. 1 Exotic grass (mean ± 1 SEM) cover during growing season one in selectively weeded experimental plots. *EG Present* and *EG Removed* indicate plots where exotic grasses remained or were removed, respectively. Likewise, *EF Present* and *EF Removed* indicate plots where exotic forbs either remained or were removed. Removals were done only in season one. Lowercase letters indicate within growing season significant differences ($P = 0.05$). Bars indicate ± 1 SEM

season, while plots established in the below-average year of 2003–2004 had less than 5% cover (Fig. 3a). These year-to-year differences in cover of native forbs reinforce the importance of yearly variation in structuring these communities (Wilson et al. 2004; Cox and Allen 2008). Seeded species were also affected by yearly variation, and some, especially the perennials, may not have established during the short timespan (2 years) of the study due to the relatively late seeding and yearly variations in timing and amounts of precipitation.

Some differences between years were probably due to the fact that plots were treated only once, when established. After treatment in the first growing season, species were allowed to recolonize the plots. Same-year recolonization, however, was minimal (Figs. 1, 2). Data from the second growing season is therefore a test of whether effects persist after treatments have ceased. Although we observed some second-year benefit to native forbs from exotic grass

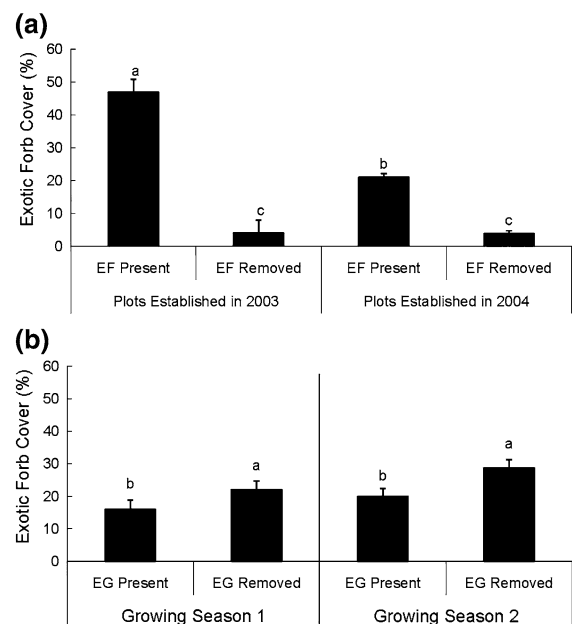


Fig. 2 Exotic forb cover (mean ± 1 SEM) in selectively weeded experimental plots: **a** effect of year of establishment and exotic forb removal during season 1. **b** Effect of exotic grass removal in both growing seasons. *EG Present* and *EG Removed* indicate plots where exotic grasses remained or were removed, respectively. Likewise, *EF Present* and *EF Removed* indicate plots where exotic forbs either remained or were removed. Removals were done only in season one. Lowercase letters indicate within growing season significant differences ($P < 0.05$). Bars indicate ± 1 SEM

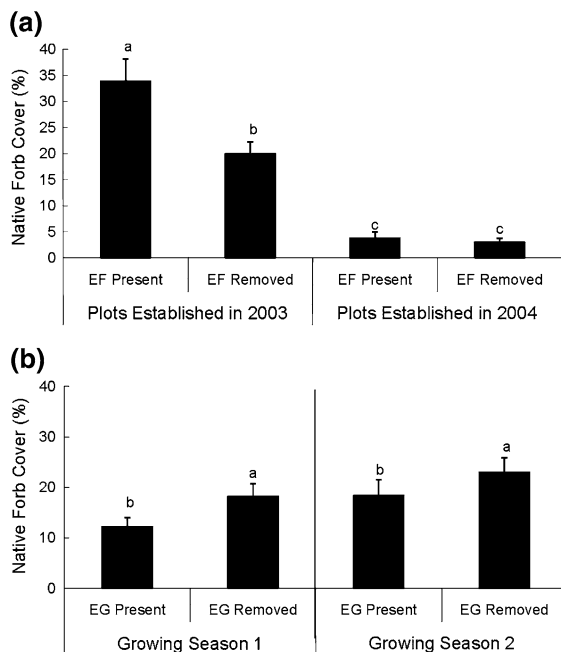


Fig. 3 Native forb cover (mean \pm 1 SEM) in selectively weeded experimental plots: **a** effect of year and exotic forb removal during season 1. **b** Effect of exotic grass removal in both seasons. *EG Present* and *EG Removed* indicate plots where exotic grasses remained or were removed, respectively. Likewise, *EF Present* and *EF Removed* indicate plots where exotic forbs either remained or were removed. Removals were done only in season one. Lowercase letters indicate significant differences ($P = 0.05$). Bars indicate \pm 1 SEM

removal, cover of exotic grasses and forbs had almost completely recovered by the second year. As has been suggested by other studies, re-application of treatments aimed at controlling exotic grasses and forbs is often required for optimal establishment of native species (Cox and Allen 2008; Gillespie and Allen 2008). However, even in the second growing season, seeded species did have greater densities in plots from which both exotic grasses and exotic forbs had been removed, similar to other studies of CSS shrubs (Eliason and Allen 1997; Cione et al. 2002).

We found that the barriers (arising from both biotic and climatic factors) to re-establishing native species in these areas are severe and may be complicated by the hierarchy of dominance between exotic grasses and exotic forbs. In this study, the density and cover of seeded species was often low, even under the best circumstances (i.e., removal of both exotic grasses and exotic forbs), because native forbs in this region are highly dependent on both

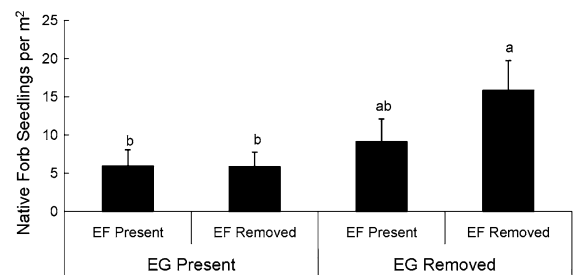


Fig. 4 Number of native forb seedlings (mean \pm 1 SEM) of species included in seed mix during the first growing season in selectively weeded experimental plots. *EG Present* and *EG Removed* indicate plots where exotic grasses either remained or were removed, respectively. Likewise, “*EF Present*” and “*EF Removed*” indicate plots where exotic forbs either remained or were removed. Removals were done only in season one. Lowercase letters indicate within growing season significant differences ($P = 0.05$). Bars indicate \pm 1 SEM

amount and timing of precipitation (Keeley et al. 2005). Therefore, seeded species were not strongly affected by the treatments and only one (*L. bicolor*) was found in more than 20% of the plots (Table 3). The exotic species were also influenced by precipitation, so that the system as a whole was limited first by precipitation, and then by the co-dominance of exotic grasses and forbs when precipitation is adequate.

From a management perspective, if increasing the density and cover of native species is desired, it may be necessary to control both the exotic grasses and the exotic forbs. Grasses can be effectively and selectively controlled through the use of grass-specific herbicides, and indeed have been controlled in this way while apparently not killing native forbs in both sagebrush-grass steppe in the Great-Basin (Nelson et al. 1970; Cox and Anderson 2004) and CSS in southern California (Cione et al. 2002; Allen et al. 2005). When grasses are controlled, however, the expansion of exotic forbs, including *Erodium* spp., may limit the ability of native species to occupy the site. Unfortunately, it is difficult to control exotic forbs without also detrimentally affecting the native forbs present at a site. For restoration efforts in southern California CSS and other semi-arid shrublands that have been invaded by both exotic grasses and forbs to be successful, managers should plan for an increase in exotic forbs when exotic grasses are removed, and also for the strong effect of varying precipitation levels on different functional groups.

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