

Mechanisms underlying the impacts of exotic annual grasses in a coastal California meadow

Heather M. Coleman · Jonathan M. Levine

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Abstract Biological invasions can impact the abundance and diversity of native species, but the specific mechanisms remain poorly discerned. In California grasslands, invasion by European annual grasses has severely reduced the quality of habitat for native forb species. To understand how introduced grasses suppress native and exotic forbs, we examined the response of a Southern California grassland community to factorial removals of live grass and the litter produced in previous seasons. To examine the role that belowground competition for water plays in mediating the impact of grasses, we crossed grass and litter removal treatments with water addition. Our results show that forbs were almost equally suppressed by both competition from live grass and direct interference by litter. Water addition did not ameliorate the effect of grass competition, suggesting that water was not the resource for which plants

compete. This evidence is consistent with the susceptibility of forbs to light limitation, especially considering that litter does not consume water or nutrients. Interestingly, despite different histories of co-occurrence with annual grass dominants, native and exotic forbs were comparably suppressed by exotic grasses. Our results indicate that suppression by both live and dead stems underlie the influence of exotic grasses on forb competitors.

Keywords Competition · Grass · Forb · Invasion · Invasive species · Santa Monica Mountains

Introduction

Exotic plant invasions incur large impacts on native species and ecosystems (Vitousek et al. 1997; Wilcove et al. 1998). Invasions have often been shown to reduce native species diversity or alter species composition (e.g. Woods 1993; Pysek and Pysek 1995; Martin 1999), but the mechanisms underlying the impacts of exotic plant invasions on native diversity are rarely elucidated. A recent review notes that competition is the process most commonly hypothesized to drive impacts, yet this is rarely tested experimentally, especially in field settings (Levine et al. 2003). A better understanding of mechanisms underlying the impacts of invasion is critical to

H. M. Coleman
Department of Ecology and Evolutionary Biology,
University of California, Los Angeles, CA 90095, USA

J. M. Levine
Department of Ecology, Evolution and Marine Biology,
University of California, Santa Barbara, CA 93106-9610,
USA

H. M. Coleman (✉)
Bren School of Environmental Science and Management,
University of California, Santa Barbara, CA 93106-5131,
USA
e-mail: hcoleman@bren.ucsb.edu

restoring native ecosystems and understanding why some invaders have larger impacts than others.

The conversion of native plant communities in California to exotic annual grasslands provides one of the most dramatic examples of habitat alteration associated with exotic plant invasion (Heady 1988). The hills and valleys of coastal California were once dominated by native perennial bunchgrasses and sage scrubland; relatively open habitats host to a diversity of native forbs occupying the space between individual bunchgrasses and shrubs (Heady 1988; Dyer and Rice 1997; Hamilton et al. 1999). However, the introduction of European annual grasses coupled with intense grazing, drought and direct human assistance has converted these habitats to the exotic grasslands that dominate the landscape today (Burcham 1957; Evans and Young 1972; Heady 1988). Along with these exotic grasses came a diversity of introduced forbs, many of which are commonly associated with exotic grasslands (Heady 1958).

The reductions in native species' performance and diversity due to grass invasion in California are well appreciated (Corbin and D'Antonio 2004). Less understood are the precise mechanisms by which grasses suppress their competitors. This is an interesting problem considering that there are two distinct ways in which we might expect exotic grasses to impact forbs, namely competition from growing shoots and roots or direct interference from litter. With respect to competition, introduced grasses tend to grow rapidly (Dyer and Rice 1997), which facilitates aboveground space occupation (Carlsen et al. 2000) and reduces light and water availability (Eliaison and Allen 1997; Dyer and Rice 1999; Hamilton et al. 1999). At the same time, a large amount of dead grass stems that blanket the soil, known as litter, is produced annually by each generation of grasses (Bartolome et al. 1980). Litter effectively occludes light and hampers some species' germination (Talbot et al. 1939; Bergelson 1990; Reynolds et al. 2001).

Although exotic grasses are well-known to impact forbs via both resource competition and the accumulation of litter (Pitt and Heady 1978; Heady 1988; Dyer and Rice 1997), the relative importance of these two mechanisms has not been examined experimentally. Doing so is critical for directing restoration efforts in California grasslands, as well as understanding how this dramatic invasion has exerted its impacts.

Understanding the individual and combined effects of grass and litter interference is also of interest because we may expect native and exotic forbs to respond differently to exotic grass interference. The native plants found in exotic grasslands are relictual species from habitats once dominated by native bunchgrasses or shrubs, not by the thick litter layer and continuous sward of vegetation that forms in exotic grasslands (Heady 1988). By contrast, many of the exotic forbs in these grasslands originate from Mediterranean pastures (Lof et al. 1995; Lavorel et al. 1998) similar to those in California today. Dominant exotic forbs such as *Erodium* have a seed morphology that facilitates burial (Stamp 1984), which may be critical for reaching the soil surface in the presence of grass litter. In addition, exotic forbs such as *Brassica nigra* germinate with the first major rainfall, allowing them to compete well with exotic annual grasses (Bell and Muller 1973). By contrast, many native annuals only emerge with the cooler rains that occur later in the season, after their grass competitors have already germinated (Levine, unpublished data).

To understand how exotic grasses dominate native and exotic forbs, we examined the response of a Southern California grassland community to factorial removals of live grass and litter. To examine the role that belowground competition for water plays in mediating the impacts of grasses, we crossed the grass and litter removal treatments with water addition. This methodology allows us to determine the response of both native and exotic forbs to various sources of grass inhibition.

Methods

All fieldwork was conducted between October 2002 and May 2003 in a meadow at the UC Stunt Ranch Reserve, in the chaparral-dominated Santa Monica Mountains of Southern California. Our study site is typical of coastal meadows that have not been deeply tilled, in that exotic grasses comprise a large portion of the flora, but share the habitat with a high cover of forbs. The mountains typically receive an annual rainfall of approximately 50–60 cm, with the vast majority falling between November and April. The amount of rain during the year of our study was slightly greater than average at 60 cm, and was

preceded by a dry year of only 27 cm. The meadow contains a variety of native and exotic forbs intermixed with European annual grasses. Table 1 shows the four grass species encountered, as well as the five most common species of native and exotic forbs out of the 28 species that were encountered in at least one of our plots. Absolute grass cover in the meadow is around 31%, while native and exotic forbs comprise about 48% cover. This mix of native and exotic species makes the habitat well suited to our study.

To examine the effects of exotic grass competition and litter suppression, 40 1.0-m² plots were divided into four 0.5 × 0.5-m² subplots, which were randomly assigned to one of four grass manipulation treatments: (1) litter removal prior to the start of the growing season; (2) grass removal, in which the exotic annual grasses were removed every two weeks following their first bout of germination; (3) both grass and litter removal; and (4) unmanipulated control.

To examine the role of competition for water in mediating competitive grass effects, half of the 40 plots were watered with 3.4 cm of simulated rain every two weeks from 28 November 2002 through 5 April 2003, while the other half were left unwatered. This watering treatment added a total of 36.7 cm of rain over the growing season, more than half the natural rainfall received over the 2002–2003 season.

In late April 2003 we visually estimated the absolute cover of each species encountered in a 0.2-m diameter circular frame centered in each subplot. All species were categorized as exotic grass, native forb or exotic forb. Native grasses were never encountered in any plot. We calculated the total summed cover of native forbs, exotic forbs, and all forbs by totaling the individual cover values of species within the appropriate groups.

The total summed cover and species richness of native, exotic, and all forbs in the various treatments

were compared using split plot analysis of variance (ANOVA). The *F*-statistic for the watering treatment, applied at the level of the plot, was calculated with a whole-plot error term. Interactions with the plot effect comprised the error terms for main and interactive effects of grass and litter treatments applied within plots (Zar 1999). Native and exotic forb cover data were arcsine transformed, while total forb cover data were log transformed to meet the normality assumption of ANOVA. The design also included a grazer exclusion treatment overlaid on half of the plots. However, it had no main or interactive effects on native, exotic, or total forb cover, and thus grazer excluded and unexcluded plots were pooled.

Results

Total forb cover, including native and exotic species, was strongly reduced by interference from both the growing exotic grasses and the litter produced by previous grass generations (Fig. 1a, Table 2). As compared to unmanipulated plots, removing both litter and grass nearly doubled the cover of forbs, and increased species richness from four to five species per subplot. Grass and litter played roughly comparable roles in this suppression, in that the removal of either alone led to an almost 1.5-fold increase in forb cover. Only litter removal, however, had a marginally significant effect on forb richness (Fig. 1b, Table 2). Water addition did not ameliorate the effects of exotic grass competition on forb cover, as the interaction between grass removal and water addition was highly nonsignificant (Table 2); nor did water show any other significant main or interactive effects.

Removal of both grass and litter roughly doubled both native and exotic forb cover (Figs. 2a, 3a). These groups were also similar in their relative sensitivity to

Table 1 Common exotic grasses and the five most common native forbs and exotic forbs in rank order abundance

Exotic grasses	Native forbs	Exotic forbs ^a
<i>Bromus hordeaceus</i>	<i>Hemizonia fasciculata</i>	<i>Erodium cicutarium</i>
<i>Bromus diandrus</i>	<i>Geranium carolinianum</i>	<i>Brassica nigra</i>
<i>Bromus madritensis</i>	<i>Lathyrus vestitus</i>	<i>Anagallis arvensis</i>
<i>Avena barbata</i>	<i>Calandrinia ciliata</i>	<i>Centaurea melitensis</i>
	<i>Plagiobothrys nothofulvus</i>	<i>Silene gallica</i>

^aOne common exotic forb is not listed in this table because the identification sample was lost

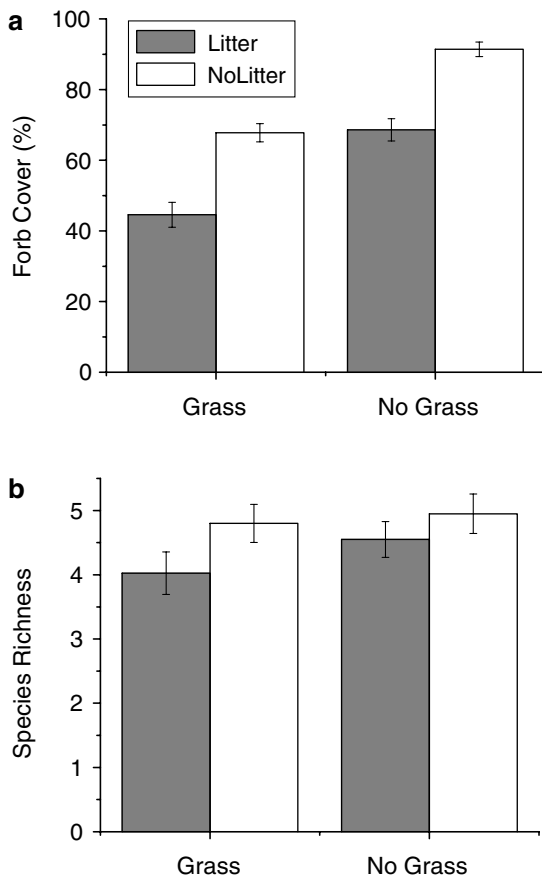


Fig. 1 (a) Cover and (b) species richness of all forbs in response to factorial removals of live exotic annual grass and its litter. Bars represent means ± 1 SE

grass and litter. As compared to unmanipulated plots, removing litter led to a significant, 1.5-fold increase in cover for both native and exotic forbs (Figs. 2a, 3a, Table 2). Native forb richness also increased significantly with litter removal, while exotic forb richness showed no response (Figs. 2b, 3b, Table 2). Removal of competitive pressure from live grass increased the cover of both native and exotic forbs 1.5-fold (Figs. 2a, 3a, Table 2), but had no effect on their richness (Figs. 2b, 3b, Table 2). Water addition did not affect native or exotic forb cover or diversity, nor did it interact with grass removal (Table 2).

Discussion

Our analysis provides insight into the mechanisms by which invasive annual grasses impact native and

exotic forb abundance and richness in a California grassland. Similar to other studies (Dyer and Rice 1997; Hamilton et al. 1999; Carlsen et al. 2000; Corbin and D'Antonio 2004), we found that exotic annual grasses strongly compete with co-occurring plants. Our factorial removal of grass and litter showed that this suppression results from both grass competition and direct interference from litter. The fractional increase due to the removal of grass and litter was comparable for forbs collectively. Effects on plant richness paralleled those on cover, but were much weaker overall.

Given that water is a limiting resource in California grasslands (Pitt and Heady 1978; Heady 1988), competition for water was expected to underlie the antagonistic effects of grasses on forbs. If competition was indeed for water, then its addition should have ameliorated, or at the very least, changed the competitive effects of grasses on forbs, resulting in a significant water addition by grass removal interaction. Instead, we found no such interaction, nor even a main effect of water addition. This suggests that exotic grass competitive suppression is mediated by changes in another resource. Light preemption (Dyer and Rice 1999) is a more likely candidate than nutrient limitation, given the similar response of forbs to grass and litter inhibition, the latter of which does not consume soil resources.

In contrast to forbs, which increased with litter removal, exotic grasses actually declined somewhat with litter removal (from 31% to 22.4% cover, $P = 0.06$). This trend probably reflects the removal of grass seed along with litter, coupled with weak litter inhibition of grasses. The significant effect of litter on forbs may then be overestimated to some extent because of the reduced grass competition that accompanies litter removal. For other reasons, however, the effect of litter may be underestimated. In addition to depleting grass seeds, litter removal also subtracts the seeds of forbs, restricting their ability to respond positively to the manipulation.

California grasslands are notoriously variable environments (Talbot et al. 1939; Heady et al. 1977), and thus one open question is whether the results we found in 2002–2003 apply to years of different climatic conditions. The rainfall over the year of our experiment was near normal for the region, and our grass and litter treatment effects remained the same with a simulated increase in rainfall. These facts

Table 2 Split-plot ANOVA results for main and interactive effects of grass removal, litter removal and water addition on all, native and exotic forbs

Source of variation	All forbs						Native forbs						Exotic forbs					
	Cover			Richness			Cover			Richness			Cover			Richness		
	d.f.	F	P	d.f.	F	P	d.f.	F	P	d.f.	F	P	d.f.	F	P	d.f.	F	P
Water addition	1	1.224	0.276	1	0.176	0.678	1	0.860	0.360	1	1.071	0.307	1	0.066	0.800	1	0.039	0.845
Whole-plot error term	38			38			38			38			38			38		
Grass removal	1	28.40	<0.001	1	1.631	0.209	1	12.80	0.001	1	0.163	0.688	1	12.95	<0.001	1	2.114	0.152
Grass × Water	1	0.204	0.655	1	0.133	0.717	1	0.498	0.485	1	1.020	0.319	1	0.199	0.658	1	0.004	0.950
Plot × Grass error term	38			38			38			38			38			38		
Litter removal	1	24.50	<0.001	1	4.395	0.043	1	21.35	<0.001	1	8.226	0.007	1	6.155	0.018	1	0.714	0.403
Litter × Water	1	0.964	0.333	1	0.488	0.489	1	0.488	0.489	1	0.455	0.504	1	0.124	0.727	1	0.342	0.562
Plot × Litter error term	38			38			38			38			38			38		
Grass × Litter	1	0.286	0.596	1	0.705	0.406	1	0.020	0.889	1	0.377	0.543	1	0.559	0.459	1	0.524	0.474
Grass × Litter × Water	1	0.391	0.536	1	0.705	0.406	1	0.961	0.333	1	0.168	0.685	1	0.022	0.882	1	0.524	0.474
Plot × Grass × Litter error term	38			38			38			38			38			38		

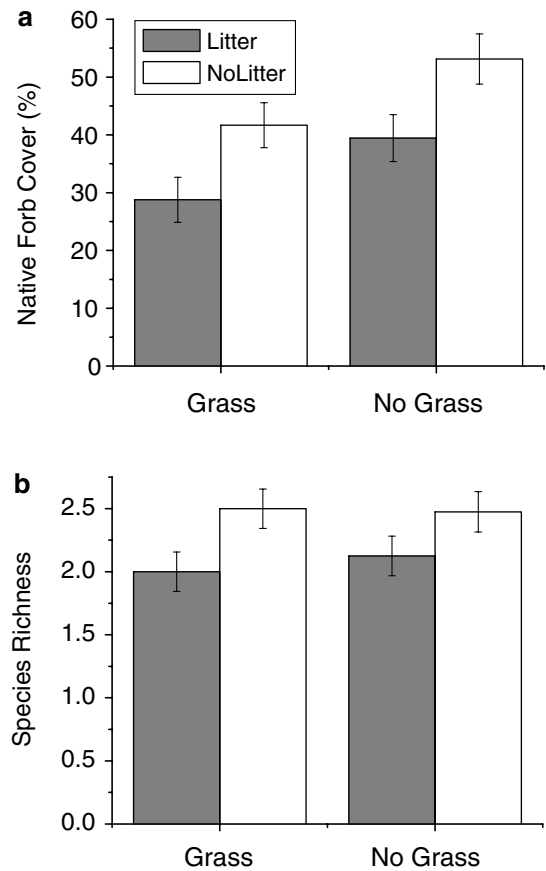


Fig. 2 (a) Cover and (b) species richness of native forbs in response to factorial removals of live exotic annual grass and its litter. Bars represent means ±1 SE

suggest that our results should apply to wetter years. Nonetheless, the year prior to our experiment was one of the lowest rainfall years on record. This is important to consider because rainfall in the previous year largely regulates the biomass of litter in the current year (Bartolome et al. 1980). It also controls the density of grass seed in the soil at the beginning of the growing season. Thus we expect that our results potentially underestimate the full impacts of exotic grasses on forbs.

Based on different histories of co-occurrence with annual grass dominants, exotic and native forbs were hypothesized to differ in their sensitivity to interference from exotic grasses. Instead, we found that these two groups experienced a similar fractional increase in cover in response to the individual and combined effects of removing litter and grass competition. Nonetheless, the native forbs currently present in

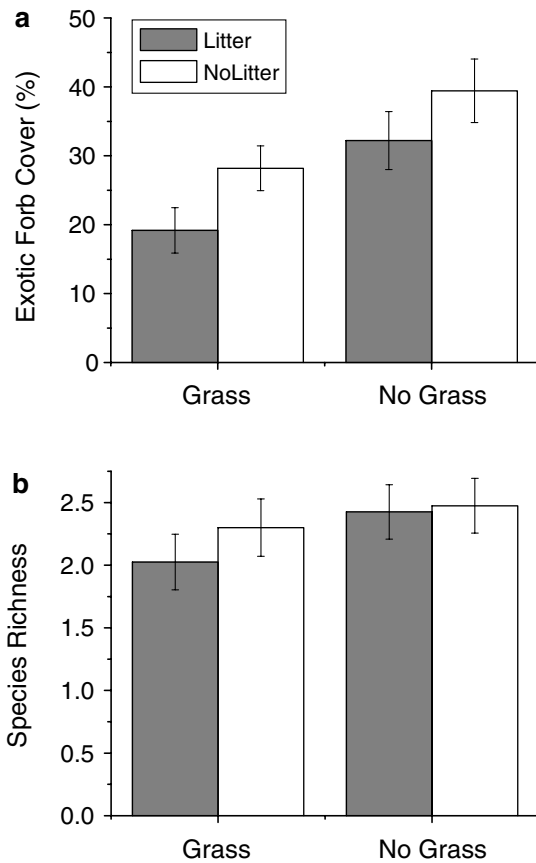


Fig. 3 (a) Cover and (b) species richness of exotic forbs in response to factorial removals of live exotic annual grass and its litter. Bars represent means ± 1 SE

California grasslands may be the subset of species better able to tolerate exotic grass competition. If those most vulnerable to the effects of European annual grasses were eliminated from exotic grasslands in the past, it may still be true that native forbs as a group are more sensitive than their exotic counterparts to annual grass competition.

With respect to improving habitat quality for native forbs, our study suggests that a one time removal of litter before the growing season may increase the cover and diversity of native forbs. A similar response would be expected with the removal of live grass, but such efforts are more difficult to implement at large scales. Moreover, in our study, litter removal also reduced grass density. Nonetheless, several important questions about the applicability of our results to restoration remain unanswered. Would similar results be found in grasslands with much greater annual grass productivity and a reduced

complement of extant forbs, as found in much of California? In addition, whether exotic forbs would eventually fill the competitive role played by annual grasses is an interesting question for future study.

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