

California native and exotic perennial grasses differ in their response to soil nitrogen, exotic annual grass density, and order of emergence

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Abstract Early emergence of plant seedlings can offer strong competitive advantages over later-germinating neighbors through the preemption of limiting resources. This phenomenon may have contributed to the persistent dominance of European annual grasses over native perennial grasses in California grasslands, since the former species typically germinate earlier in the growing season than the latter and grow rapidly after establishing. Recently, European perennial grasses have been spreading into both non-native annual and native perennial coastal grass stands in

California. These exotic perennials appear to be less affected by the priority effects arising from earlier germination by European annual grasses. In addition, these species interactions in California grasslands may be mediated by increasing anthropogenic or natural soil nitrogen inputs. We conducted a greenhouse experiment to test the effects of order of emergence and annual grass seedling density on native and exotic perennial grass seedling performance across different levels of nitrogen availability. We manipulated the order of emergence and density of an exotic annual grass (*Bromus diandrus*) grown with either *Nassella pulchra* (native perennial grass), *Festuca rubra* (native perennial grass), or *Holcus lanatus* (exotic perennial grass), with and without added nitrogen. Earlier *B. diandrus* emergence and higher *B. diandrus* density resulted in greater reduction in the above-ground productivity of the perennial grasses. However, *B. diandrus* suppressed both native perennials to a greater extent than it did *H. lanatus*. Nitrogen addition had no effect on the productivity of native perennials, but greatly increased the growth of the exotic perennial *H. lanatus*, grown with *B. diandrus*. These results suggest that the order of emergence of exotic annual versus native perennial grass seedlings could play an important role in the continued dominance of exotic annual grasses in California. The expansion of the exotic perennial grass *H. lanatus* in coastal California may be linked to its higher tolerance of earlier-emerging annual grasses and its ability to access soil resources amidst high densities of annual grasses.

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Introduction

The order of emergence among competitors affects the growth, survival, and fecundity of plants across a wide range of species, especially in situations with well-defined growth windows and high densities of competitors (Miller et al. 1994; Verdù and Traveset 2005). Early emergence in relation to competitors can allow preemption of available resources by the early emerging species, yielding disproportionate advantages (Ross and Harper 1972). Once established, the early-emerging species may maintain dominance even if it is a relatively poor competitor during later life-stages.

Priority effects have been well documented in grasses (Harper 1961; Ross and Harper 1972; Miller 1987; D'Antonio et al. 2001), and may be of particular importance in maintaining the current structure of California grasslands. These grasslands have experienced extensive invasion by exotic annual grasses and steep declines in native perennial bunchgrasses over the last two centuries (Heady 1988; D'Antonio et al. 2007). The continued success of exotic annual grasses suggests some competitive advantage over native perennial grasses (Dyer and Rice 1997; Hamilton et al. 1999; Corbin et al. 2007), although the two groups coexist in some coastal prairie sites (Heady et al. 1988; Stromberg et al. 2001). Several studies have shown that mature native perennial grasses can successfully compete with exotic annuals (e.g. Peart 1989b; Seabloom et al. 2003; Corbin and D'Antonio 2004b; Lulow 2006), but the natives may be sensitive to competition with annual plants at the seedling stage, particularly because exotic annual grasses tend to emerge at much higher densities and earlier than native perennial grasses (Dyer and Rice 1997; Hamilton et al. 1999; Humphrey and Schupp 2004; DiVittorio et al. 2007). Exotic annual grasses germinate days after the first fall or winter rains, while native perennial grasses are typically slower to germinate (e.g., Reynolds et al. 2001). Subsequent aboveground production of exotic annual grasses outpaces that of native perennial grasses, potentially reducing light, water, and nutrients available for

emerging perennial seedlings (Jackson and Roy 1986; Dyer and Rice 1999). While some native bunchgrass adults are thought to be long-lived (Hamilton et al. 1999), they can eventually succumb to drought, burrowing animals, or other mortality sources. If they cannot successfully recruit due to seedling competition from exotic annual grasses, then populations should eventually decline.

Efforts to reintroduce native perennial bunchgrasses have had limited success when annuals are present at their typical high densities (Wilson and Gerry 1995; Clausnitzer et al. 1999; Dyer and Rice 1999; Brown and Rice 2000). Management strategies that negate priority effects and reduce the strength of annual grass competition via reduced performance or density should improve the survival of perennial grass seedlings and increase the success of restoration efforts (Corbin et al. 2004). For example, supplementing native seed supply (Seabloom et al. 2003), killing annual grasses or their seeds (Stromberg and Kephart 1996; Moyes et al. 2005), or the planting of native perennial grasses as seedling plugs rather than seeds (Dyer et al. 1996; Buisson et al. 2006) increases native grass establishment in restoration sites, demonstrating the strong role exotic annual seedling density plays in the suppression of native perennial grass establishment.

Beyond the competitive advantage gained by exotic annual grasses via earlier and abundant germination, grassland restoration efforts in California also need to deal with large increases in soil nitrogen availability due to atmospheric nitrogen deposition and colonization by nitrogen-fixing shrubs (Maron and Connors 1996; Vitousek et al. 1997; Weiss 1999, 2006; Fenn et al. 2003; Haubensak et al. 2004; Dise and Stevens 2005). Increases in soil nitrogen availability are hypothesized to confer a competitive advantage to fast-growing exotic species (Vitousek et al. 1987; Huenneke et al. 1990; Burke and Grime 1996), and appear to disproportionately benefit exotic annual grasses in California (e.g., Huenneke et al. 1990; Maron and Connors 1996; Kolb et al. 2002; Lowe et al. 2003). For example, encroachment by non-native annual grasses onto serpentine-derived soils, long a refuge from exotic annual grass competition for many California native grassland species, occur when soil nitrogen levels become elevated (Huenneke et al. 1990; Weiss 1999). Continued increases in nitrogen deposition predicted through the next century (Phoenix et al. 2006; Weiss

2006) could have widespread consequences for patterns of exotic species invasion and spread. Restoration strategies in California coastal grasslands will need to include the direct and indirect effects of soil nitrogen enrichment on native perennial grass versus exotic annual grass performance.

Even as restoration efforts to reestablish native perennial grasses continue, exotic perennial grasses such as *Holcus lanatus*, *Festuca arundinaceae*, and *Phalaris aquatica* have begun a second transformation of some areas in western grasslands (Elliott and Wehausen 1974; Foin and Hektner 1986; Peart 1989a; Ewing 2002). The ability of exotic perennial grasses to colonize the same annual-dominated stands that have excluded native perennial reestablishment (Foin and Hektner 1986; Peart 1989c) suggests that at least some European perennial grass species are less susceptible to priority effects and competition from annual grasses. Given the shared life-history of California and European perennial bunchgrasses, the differential success of exotic versus native perennials may be linked to subtle differences in reproductive output, germination timing, or seedling growth traits, or responses to soil nitrogen enrichment. For example, *Holcus lanatus*, a common exotic perennial invader in mesic coastal grassland, producing copious seed (Peart 1989a), has higher relative growth rates than some California native perennial grass species (Thomsen et al. 2006a; Corbin and D'Antonio, unpublished data), and appears to be highly responsive to nitrogen enrichment (Schippers et al. 1999; Thomsen et al. 2006a). This species may thus be less hindered than native perennial grasses by rapidly germinating exotic annuals or high soil nitrogen availability at the seedling stage. Comparisons of the performance of native versus exotic perennial grass seedlings when faced with soil nitrogen enrichment or competition with exotic annual grasses may help explain the disparity in their ability to colonize annual dominated grasslands.

Our objective in this study was to determine the importance of annual grass emergence time and density to the growth of native and exotic perennial grass seedlings with and without nitrogen addition. We hypothesized that:

- (1) Reversing the typical “annual-followed-by-perennial grass” order of emergence should increase perennial (native and exotic) grass seedling growth by negating the priority effect.
- (2) Performance of the native perennial grass seedlings should be reduced to a greater extent than that of exotic perennial grass seedlings when grown with high densities of exotic annual grasses.
- (3) The negative impact of exotic annual grasses on native perennial grasses should be greater with added nitrogen because of the greater ability of annuals to respond rapidly to increased resource availability. In contrast, N addition should either have no effect or benefit exotic perennials grown with exotic annuals.

We tested these hypotheses in a greenhouse using grass seedlings grown from seed. We experimentally manipulated annual grass emergence time, annual grass density, and soil nitrogen availability and tracked the performance of native and non-native perennial grasses.

Materials and methods

Study species and source population description

We chose *Nassella pulchra* A. Hitchcock (Barkworth), *Festuca rubra* L., and *Holcus lanatus* L. as the target perennial species, and *Bromus diandrus* Roth as the annual competitor. Henceforward, the grasses will be referred to by their generic names; all nomenclature follows Hickman (1993). These grass species co-occur in their ranges in California (Hickman 1993). *Nassella* is a native perennial grass that was historically abundant throughout California (Heady 1988), is among the most common native bunchgrasses today in the California Floristic Province (Bartolome and Gemmill 1981), and is a widely used species in grassland restoration. *Festuca* is a coastally restricted species that remains abundant in some remnant prairies (Stromberg et al. 2001). *Holcus* is an exotic perennial invader in mesic coastal and inland California grasslands, encroaching on both non-native annual dominated and remnant native perennial patches (Peart 1989a; Corbin et al. 2007). *Bromus* is a widespread Eurasian species that appears to be a strong competitor in California annual grasslands (Wilken and Painter 1993), particularly in more nitrogen-rich sites (Maron and Jefferies 1999; Rice and Nagy 2000; Hoopes and Hall 2002).

We collected seeds of all of the species at Tom's Point Preserve (38°13' N, 122°57' W), a private nature reserve near Tomales, CA, USA. The site has been the location for a number of field studies focused on competition and resource use of native perennial, exotic perennial, and exotic annual grasses (e.g. Corbin and D'Antonio 2004a, b; Corbin et al. 2005; DiVittorio et al. 2007). The vegetation is a mosaic of exotic annual, native perennial, or exotic perennial species with large patches of *Holcus* and *Bromus*.

Experimental design

We conducted the experiment in the Oxford Tract Greenhouse at the University of California, Berkeley from March 8, 2002 to June 4, 2002 under ambient temperature conditions. We arranged the experiment in a randomized full factorial design, with the following fixed factors: focal perennial species (*Nassella*, *Festuca*, *Holcus*), *Bromus* density (low, high), nitrogen availability (low, high), and *Bromus* emergence time (simultaneous, delayed). All pots were mixed species in that they had *Bromus* with three individuals of one of the perennial grass species. In addition to the mixed species pots, we planted perennial grasses in monoculture (three individuals) and crossed the monoculture treatments with nitrogen availability to measure perennial grass response without interspecific competitors. The monoculture pots with ambient nitrogen treatment for each perennial species served as a baseline of growth for that species (see below). We replicated each treatment eight times.

Using 50% fine sand and 50% peat moss soil mix (UC mix), we planted seeds of a given focal species (*Nassella*, *Festuca*, or *Holcus*) in each perennial treatment pot (10 l, 20-cm diameter). After emergence, we thinned the germinated plants in each pot to three seedlings spaced a minimum of 5 cm from each other and the side of the pot. We transplanted additional seedlings to pots with fewer than three emerged perennials.

We planted *Bromus* seeds either concurrently with the planting of the perennial seeds ("simultaneous") or 14 days afterward ("delayed"). This design allowed us to evaluate how variation in early seedling growth timing interacts with exotic annual density and identity of the competitor (perennial species).

We planted *Bromus* at two densities: "high" (1,592 seeds m⁻², 50 seeds/pot) and "low" (637 seeds m⁻²,

20 seeds/pot). We based our high-density treatment on the density of annual seeds found in an equivalent area of *Bromus* dominated stands at Tom's Point preserve (DiVittorio et al., unpublished data) and elsewhere in the state (Young et al. 1981). The low-density treatment was meant to approximate annual grass seed densities reduced by management, but is not based on field measurements.

In order to create the "high" soil nitrogen treatment, we added 0.93 g of blood meal (Green All 100% Organic Blood Meal; 13-0-0) to the wet soil surface in three doses (0, 30, 60 days after perennial planting). This "high" level of nitrogen addition (10 g N m⁻² over the course of the experiment) is consistent with the estimates of soil nitrogen input by nitrogen fixing shrubs in some coastal grasslands (Maron and Jefferies 1999; Haubensak et al. 2004) and falls within the range of nitrogen fertilization used in previous grassland studies (e.g., Inouye and Tilman 1988). No nitrogen was added to the "low" soil nitrogen treatment.

We positioned pots randomly with respect to treatment in the greenhouse, and rotated within and between benches every 2 weeks. We watered plants to soil saturation three or four times per week. At the first appearance of a developing *Bromus* flowering culm, we destructively sampled all plants by cutting at the soil surface and separated material by species. After drying the aboveground plant material in an oven at 70°C for 2 days, we recorded the mean individual dry biomass of each species by pot.

Statistical analysis

We converted biomass measurements into an index of relative shoot yield per plant (RYP), calculated as the perennial biomass in an experimental treatment divided by the mean biomass of the conspecific monoculture treatment plants in ambient nitrogen (hereafter referred to as control): $RYP = \text{Biomass}_{\text{experimental}} / \text{Mean Biomass}_{\text{control}}$. This index allowed us to compare across the perennial grasses in evaluating the relative effect of the treatments on their growth (Johansson and Keddy 1991).

We performed all statistical tests with SYSTAT 11.0 (Systat Software, Inc.). Our analysis began with a general assessment of the impact of *Bromus* on perennial grass performance using a series of one-sample *t*-tests. We conducted one *t*-test for each

species to compare the actual growth in competition with *Bromus* to growth in a hypothetical null model ($RYP = 1$). Competitive treatments were pooled across *Bromus* density, *Bromus* emergence time, and nitrogen addition. We then determined the effect of nitrogen availability on perennial species growth in monoculture with a two-factor ANOVA, using species identity and nitrogen availability as independent fixed factors. We evaluated the independent and interactive effects of *Bromus* density, emergence timing, nitrogen availability, and perennial species identity with a separate four-factor analysis of variance (ANOVA). We used Tukey HSD post-hoc tests ($\alpha = 0.05$) to make any appropriate pair-wise comparisons in the four and two-factor ANOVA tests.

The RYP data used in the *t*-tests were log transformed to improve normality before analysis. Prior to application of the ANOVA tests, we applied Cochran's test for unequal variances to the raw data to assess its heteroscedacity. The subset of biomass data used in the two-way ANOVA passed Cochran's test, and so was left untransformed. The RYP data used in the four-factor ANOVA failed Cochran's test. We again performed a log transformation to both normalize the data and reduce heteroscedacity. The transformed RYP data did not pass the test, but was closer to the given critical value. Because a balanced design ANOVA, such as that employed in this study, is robust to minor departures from homogeneity of variances (Underwood 1997; McGuinness 2002), we proceeded with the four-factor ANOVA on the transformed data. We present back-transformed data and errors in figures when data were transformed for analysis.

Results

Perennial response to *Bromus* presence

Growth of all three perennial species was suppressed in the presence of *Bromus*. When compared to the hypothetical control RYP value of 1, the above-ground production of *Holcus* ($t = -9.983$, $df = 58$, $P < 0.0001$), *Nassella* ($t = -17.381$, $df = 63$, $P < 0.0001$), and *Festuca* ($t = -23.150$, $df = 63$, $P < 0.0001$) was significantly reduced when grown with *Bromus*. However, the degree to which *Bromus*

affected perennial growth differed among species. Competitive treatments reduced *Holcus* growth by nearly 75%. The two native perennials experienced even greater suppression: *Nassella* growth was reduced by 85%, while *Festuca* growth was reduced by 95% (Fig. 1).

Perennial response to nitrogen addition in monoculture

Nitrogen availability significantly interacted with perennial grass species identity in the monoculture treatments (Table 1a). *Holcus* and *Festuca*, but not *Nassella*, responded to nitrogen addition with increased aboveground growth (Fig. 2). *Holcus* grew significantly larger than the other two perennial species: in both the ambient and added nitrogen treatments, *Holcus* growth surpassed *Festuca* and *Nassella*, while the aboveground production of the two native grasses was statistically indistinguishable (Fig. 2).

Perennial response to varying *Bromus* density, nitrogen addition, and order of emergence

There were two significant three-way interactions in the four-factor ANOVA: (1) Perennial sensitivity to *Bromus* density varied with nitrogen addition and order of emergence and (2) Perennial species identity interacted with *Bromus* density and nitrogen addition

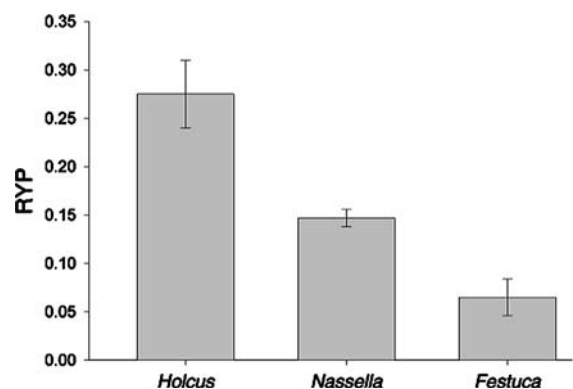


Fig. 1 Relative shoot yield of perennials (RYP) in response to competition with *Bromus*, averaged across all *Bromus* density, nitrogen, and *Bromus* emergence time treatments (mean \pm 1 SE). An RYP below 1 suggests a reduction in growth with *Bromus* competitors relative to growth in monoculture

Table 1 Summary of two-factor and four-factor ANOVA tests (a) Two-factor ANOVA: effect of perennial species identity (PS) and nitrogen availability (N) on aboveground production. (b) Four-factor ANOVA: effects of perennial species identity (PS), *Bromus* emergence time (BET), *Bromus* density (BD), and nitrogen availability (N) on relative shoot yield per plant

Treatment	df	Mean-square	F	P
<i>(a) Two-factor ANOVA</i>				
Perennial species	2	47.808	161.19	<0.001
Nitrogen	1	6.695	22.573	<0.001
PS × N	2	1.841	6.209	0.004
Error	40	0.297		
<i>(b) Four-factor ANOVA</i>				
Perennial species	2	45.797	32.823	<0.001
<i>Bromus</i> emergence time	1	296.475	212.490	<0.001
<i>Bromus</i> density	1	26.100	18.707	<0.001
Nitrogen	1	7.133	5.113	0.025
PS × BET	2	4.573	3.278	0.040
PS × BD	2	0.160	0.115	0.892
PS × N	2	15.665	11.228	<0.001
BET × N	1	0.211	0.151	0.698
BET × BD	1	0.841	0.603	0.439
BD × N	1	5.412	3.879	0.051
PS × BET × BD	2	0.467	0.335	0.716
PS × BET × N	2	3.722	2.668	0.072
PS × BD × N	2	5.012	3.592	0.030
BET × BD × N	1	7.240	5.189	0.024
PS × BET × BD × N	2	1.463	1.049	0.353
Error	162	1.395		

Significant results are in bold

(Table 1b). These interactions are discussed in detail below.

Bromus density × nitrogen addition × order of emergence

Delayed *Bromus* emergence significantly increased the productivity of the perennial grasses (Table 1b). Positive production responses by the perennials in delayed *Bromus* emergence treatments occurred at both *Bromus* densities although the “release” was stronger at low *Bromus* density (Fig. 3). Nitrogen addition had no effect on this pattern. High *Bromus* density generally resulted in lower perennial grass growth, although the effect was negated in the simultaneous *Bromus* emergence pots with added nitrogen (Fig. 3).

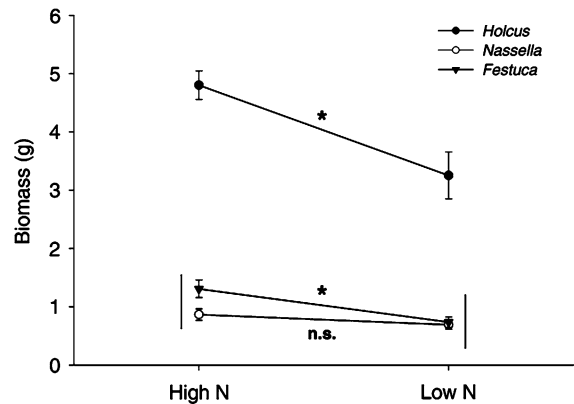


Fig. 2 Perennial aboveground growth in monoculture with and without nitrogen addition (mean \pm 1 SE). Vertical lines indicate non-significant differences within a given nitrogen treatment. Asterisks indicate differences within a single species across nitrogen treatments; “n.s.” indicates non-significance

Perennial species identity × *Bromus* density × nitrogen addition

The three perennials differed greatly in their responses to reduced *Bromus* density and increased nitrogen availability (Table 1b). In the high nitrogen treatment, *Holcus* RYP was significantly greater than that of *Nassella* or *Festuca* at both high and low *Bromus* density (Fig. 4). *Nassella* and *Festuca*, the two native species, responded similarly to each other in the high nitrogen treatment. In contrast, in the low nitrogen treatment, *Nassella* outperformed *Festuca*, and at the high *Bromus* density, outperformed *Holcus*. In the low *Bromus* density treatment, *Holcus* and *Nassella* RYP were similar, while *Festuca* RYP was significantly lower (Fig. 4).

Overall, *Holcus* experienced the least growth in the high *Bromus* density, low nitrogen level treatment (Fig. 4). Reduced *Bromus* density and increased soil nitrogen availability tended to increase *Holcus* performance (Fig. 4). Like *Holcus*, *Festuca* exhibited the least growth in the high *Bromus* density treatment at the lower nitrogen level. Although *Festuca* growth increased in the low *Bromus* density treatment, overall, *Festuca* experienced the most consistent suppression by *Bromus* of the three perennial grasses (Fig. 4). In contrast to *Holcus* and *Festuca*, *Nassella* experienced its lowest level of growth in high *Bromus* density with high soil nitrogen. *Nassella* RYP was significantly increased with reductions in either nitrogen availability or *Bromus* density.

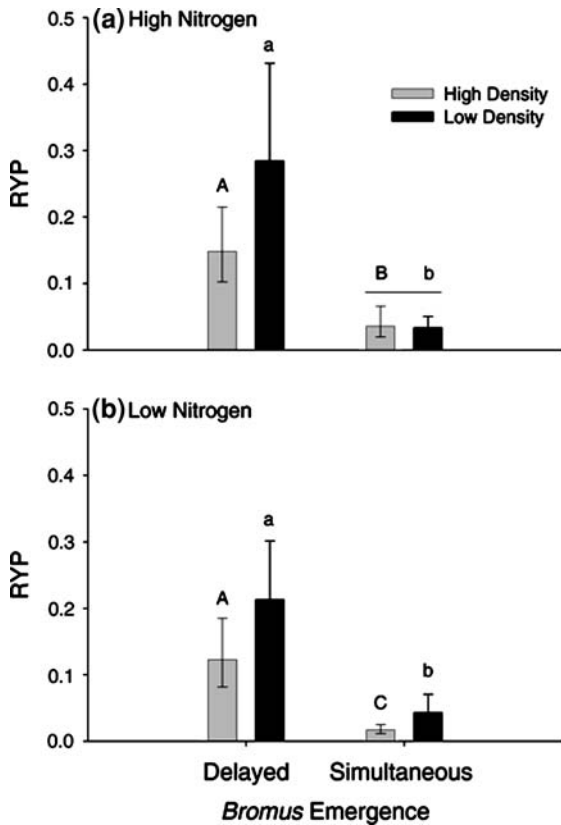


Fig. 3 Relative shoot yield of perennials (RYP) in high and low *Bromus* density treatments at simultaneous and late *Bromus* emergence times, separated by nitrogen addition treatment (mean \pm 1 SE). Horizontal lines indicate non-significant differences within a given density and emergence time treatment combination. Shared letters indicate non-significant differences within a given density of *Bromus* across nitrogen addition and emergence time treatment combinations

Discussion

This study gauged the importance of density and timing of emergence of an abundant annual grass on potentially coexisting perennial grasses under different levels of soil fertility. The annual grass competitor *Bromus* suppressed growth of all three perennial species relative to their growth in monoculture. As predicted, the level of suppression tended to increase with *Bromus* density and decrease when perennial grasses emerged before *Bromus*. Nitrogen addition increased the suppression of one native perennial by *Bromus*, while the other native perennial showed no response. Suppression of the exotic perennial by *Bromus* decreased with nitrogen addition.

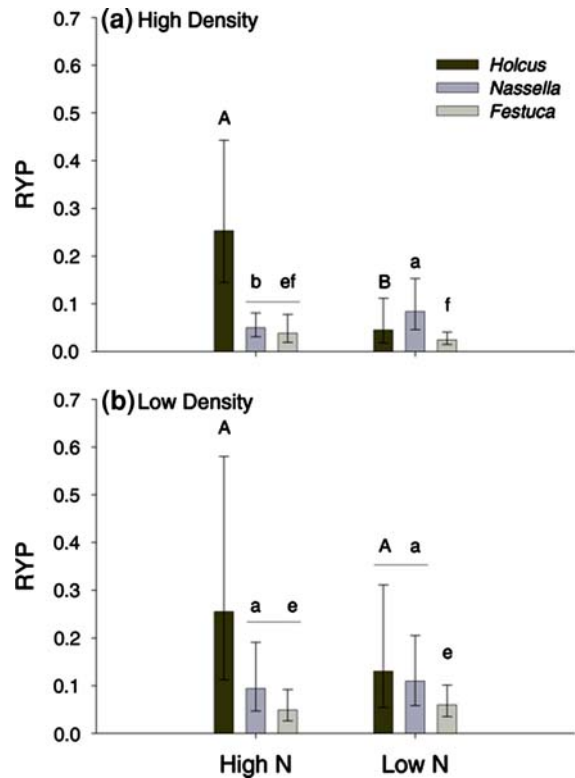


Fig. 4 Relative shoot yield of perennials (RYP) with and without nitrogen addition, separated by *Bromus* density treatment (mean \pm 1 SE). Horizontal lines indicate non-significant differences within a given density and nitrogen treatment combination. Shared letters indicate non-significant differences within a single species across all density and nitrogen treatment combinations

Order of emergence and density impacts on native perennial grass seedling growth

Both the native and exotic perennial grasses responded strongly to delays in *Bromus* emergence, increasing relative yield per plant (RYP) up to eight-fold (Fig. 3). The reduced *Bromus* density treatment similarly increased perennial grass RYP. The strength of these responses demonstrates the potential importance of the timing of emergence for perennial grass seedlings and supports the findings of previous studies in California grasslands and other semi-arid grassland systems that highlight the sensitivity of the seedling stage in perennial grasses (Bartolome and Gemmill 1981; Dyer et al. 1996; Dyer and Rice 1997; Clausnitzer et al. 1999; Hamilton et al. 1999; Brown and Rice 2000; Humphrey and Schupp 2004; Lenz and Facelli 2005). California native perennial grasses

must survive the summer drought, and accordingly, invest less in their aboveground growth or reproductive efforts in the first year than do exotic annual grasses (Jackson and Roy 1986; Holmes and Rice 1996). Annual grasses, on the other hand, must complete their life cycle before California's annual summer drought and so are among the earliest plants to germinate following the onset of the rainy season. The high seedling densities and rapid aboveground growth exhibited by exotic annual grasses create an intense competitive environment for later emerging seedlings (Jackson and Roy 1986; Corbin et al. 2007).

Priority effects have been reported in numerous systems across a broad range of taxonomic groups (e.g., Harper 1961; Lawler and Morin 1993; Shorrocks and Bingley 1994; D'Antonio et al. 2001; Kennedy and Bruns 2005). In California grasslands, established native perennial stands are generally resistant to invasion by exotic annual grasses (Seabloom et al. 2003; Corbin and D'Antonio 2004b; Lulow 2006), representing a priority effect manifested through arrival in a previous growing season. However, priority effects for exotic annual grasses competing with perennial seedlings occur over much shorter time scales. Previous work has shown that differences in emergence timing of even a few days can be enough to reverse competitive hierarchies between similar grass types (Harper 1961; Ross and Harper 1972; Rice and Dyer 2001). Some grasses, including *Nassella*, may even accelerate emergence in response to annual grass neighbors, presumably to minimize the impacts of later emergence (Dyer et al. 2000). Here, we demonstrate the strong priority effects that annual grasses can have on the seedlings of potentially coexisting perennial grasses; reversing the order of emergence of the grass types had a large effect on perennial grass seedling productivity, even when greatly outnumbered by an exotic annual grass.

Early emergence and high densities of exotic annual seedlings are obstacles that must be overcome for the restoration and maintenance of native-dominated grasslands (Stromberg et al. 2007). Successful restoration of native perennial grasslands often employs at least one of three strategies that improve perennial seedling performance: increasing native seed input (e.g., Seabloom et al. 2003), decreasing annual grass seed input/germination (e.g., Moyes et al. 2005), or planting plugs of native perennial grasses rather than starting them from seed (e.g.,

Dyer et al. 1996; Huddleston and Young 2004). The first two strategies reduce the relative abundance of exotic annual grasses, while the last, in effect, reverses the order of emergence of exotic annual and native perennial grasses.

Once established, some stands of native perennials are able to exclude annual grass invasion (Corbin and D'Antonio 2004b), and some studies suggest that native perennial grasses are stronger per-capita competitors than exotic annual grasses (e.g., Seabloom et al. 2003; DiVittorio et al. 2007). However, the high rate of soil turnover in California grasslands due to gopher and feral pig disturbance will create numerous opportunities for exotic annual grasses to compete with native perennial seedlings within restoration projects over the long-term (Hobbs and Mooney 1985; Kotanen 1995; Stromberg and Griffin 1996). Given that exotic annual propagule supply grossly exceeds that of native perennials, asymmetry in competition through emergence timing and density will likely limit the long-term ability of native perennial grasses to reestablish dominance in restored areas unless disturbance is minimized.

Nitrogen addition impacts on native perennial grass seedling growth

Differential responses to nitrogen addition between the two native perennial grass species point toward differences in their ability to access this resource amidst abundant exotic annual grass cover. *Nassella* in the monoculture treatment did not increase aboveground growth following nitrogen addition, which suggests that it was not nitrogen limited in this study. Alternatively, the response could have been reflected by reduced investment in belowground growth (Chapin 1980), which we did not measure in this study. However, *Nassella* root:shoot did not decrease with nitrogen fertilization in another study (Thomsen et al. 2006a). When nitrogen was added to *Nassella* grown with a high density of *Bromus*, *Nassella* experienced a relative decrease in aboveground growth. *Festuca*, on the other hand, did exhibit a positive growth response to nitrogen addition in monoculture, demonstrating that it was nitrogen limited. However, *Festuca* showed no response to nitrogen addition when grown with *Bromus*, suggesting that *Festuca* was unable to benefit from added nitrogen with neighboring annuals

present. The responses of both *Nassella* and *Festuca* are consistent with an indirect negative relationship between soil nitrogen and native perennial grass performance due to increased productivity of exotic annual grasses.

Our findings complement a number of studies in California and other semi-arid grasslands which found that exotic annual grasses benefit disproportionately from soil nitrogen supplementation relative to native perennial grasses (e.g., Huenneke et al. 1990; Maron and Connors 1996; Claassen and Marler 1998; Prober et al. 2002; Lowe et al. 2003; Abraham et al., unpublished data; but see Kolb and Alpert 2003). This suggests that native perennial grass seedlings are less likely to establish when faced with both exotic annual grass competition and persistent or increasing soil nitrogen enrichment. While this does not bode well for grassland restoration efforts, Seabloom et al. (2003) found that, with seed supplementation, perennial grass seedlings were capable of establishing in stands of exotic annual grasses across a gradient of nitrate availability. However, their exotic annual grass stands were not dominated by *Bromus diandrus*; it is possible that the identity of the annual grass competitor plays a role in determining the outcome of perennial grass seedlings. Corbin and D'Antonio (2004a) showed a first year reduction in annual grass suppression of native perennial seedlings after soil amendment with sawdust (to reduce available soil nitrogen), but found that there was no long-term benefit to the native grasses. Active management of soil nitrogen levels may prove to be less important for maintenance of native perennial dominated grasslands than reducing the density of exotic annual grass competitors (DiVittorio et al. 2007).

Comparison of exotic and native perennial grass seedling response

Productivity, tolerance of annual grass competition, and response to resource pulses differed significantly between native and exotic perennial grasses in this study. While each perennial species responded to the inclusion of *Bromus* with marked reductions in growth, *Holcus* tended to be less affected than either native perennial. Relative to *Festuca*, *Holcus* suffered a smaller overall reduction in growth in every treatment combination. In low nitrogen conditions,

Nassella RYP was equal to or greater than *Holcus* RYP. However, *Nassella* RYP was lower than that of *Holcus* at a higher soil nitrogen level. Additionally, *Holcus* productivity was much greater than that of either native perennial in monoculture (Fig. 2).

A field study of *Holcus* establishment in exotic annual grasslands found that *Holcus* seedling growth was not affected by competition with annual grasses (Thomsen et al. 2006b). Thomsen et al. (2006a) also demonstrated that *Holcus* has much higher initial relative growth rates than native perennial grasses, under both high and low nitrogen conditions. Individual size in grasses is often positively correlated with survival likelihood and competitive ability (Davies et al. 1999; Ewing 2002; Page and Bork 2005). As such, even if exotic annual grasses suppressed *Holcus*, *Festuca*, and *Nassella* equally, *Holcus* would likely be better able to compete with other grassland species due to its faster growth rate and larger size. Given the results of this study and that of Thomsen et al. (2006b), it is likely that *Holcus* seedlings better establish in exotic annual grass dominated stands than do native perennials.

Unlike the two native perennials, *Holcus* growth increased with additions of nitrogen both in monoculture and in combination with *Bromus*, suggesting that *Holcus* is a relatively strong competitor for soil resources with *Bromus*, at least when water is not limiting as in this study. This response was mirrored in a field study; elevated light and nutrient availability due to gopher disturbance increased *Holcus* colonization relative to an exotic annual, *Vulpia bromoides* (Peart 1989c). *Holcus* also showed increased productivity with higher nitrogen availability while in competition with native perennial grasses (Schippers et al. 1999; Ewing 2002; Thomsen et al. 2006a); therefore, it appears to be not only highly responsive to nitrogen enrichment, but also able to access that nitrogen alongside a range of potential competitors.

Implications for management

California's annual-dominated grasslands have excluded native perennial grasses for decades, but in the coastal zone, they are often colonized by a number of exotic perennial bunchgrass species; this suggests that there are critical differences between traits of these native and exotic perennial grasses. In

this study, the native and exotic perennial grasses we investigated responded differently to both soil fertilization and competition with exotic annual grasses. Currently, common strategies for native grass management are based on mitigating the emergence of exotic annual grasses, and the associated negative effects of nitrogen enrichment that accompany their high density and rapid growth. However, management tools to specifically limit the encroachment of exotic perennial grass are largely undeveloped, and the efficacy of current management techniques on limiting their spread is not well known (Stromberg et al. 2007). Management practices that reduce annual grass seedling density could inadvertently increase the abundance of *Holcus*, particularly in areas with high soil nitrogen availability. As European perennial grasses become increasingly abundant and widespread in California coastal grasslands, land management based on generalizable life history differences among native perennial and exotic annual grasses will lose efficacy. Successful management of native grassland species will require continued research into the traits of a wider range of native and exotic bunchgrasses and their species-specific responses to current restoration practices and future environmental conditions.

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