The effect of soil nitrogen on competition between native and exotic perennial grasses from northern coastal California

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Abstract

The invasion of European perennial grasses represents a new threat to the native coastal prairie of northern California. Many coastal prairie sites also experience anthropogenic nitrogen (N) deposition or increased N availability as a result of invasion by N-fixing shrubs. We tested the hypothesis that greater seedling competitive ability and greater responsiveness to high N availability of exotic perennial grasses facilitates their invasion in coastal prairie. We evaluated pairwise competitive responses and effects, and the occurrence of asymmetrical competition, among three common native perennial grasses (*Agrostis oregonensis*, *Festuca rubra*, and *Nassella pulchra*) and three exotic perennial grasses (*Holcus lanatus*, *Phalaris aquatica*, and *Festuca arundinacea*), at two levels of soil N. We also compared the root and shoot biomass and response to fertilization of singly-grown plants, so we could evaluate how performance in competition related to innate plant traits. Competitive effects and responses were negatively correlated and in general varied continuously across native and exotic species. Two exceptions were the exotic species *Holcus*, which had large effects on neighbors and small responses to them, and competed asymmetrically with all other species in the experiment, and the native grass *Nassella*, which had strong responses to but little effect on neighbors, and was out-competed by all but one other species in the experiment. High allocation to roots and high early relative growth rate appear to explain *Holcus*'s competitive dominance, but its shoot biomass when grown alone was not significantly greater than those of the species it out-competed. Competitive dynamics were unaffected by fertilization. Therefore, we conclude that seedling competitive ability alone does not explain the increasing dominance of exotic perennial grasses in California coastal prairie. Furthermore, since native and exotic species responded individualistically, grouping species as 'natives' and 'exotics' obscured underlying variation within the two categories. Finally, elevated soil N does not appear to influence competition among the native and exotic perennial grasses studied, so reducing soil N pools may not be a critical step for the restoration of California coastal prairie.

Introduction

European annual grasses and forbs have almost completely replaced native perennial grasses in many of California's grasslands. One exception to this rule is the coastal prairie of northern California, in which native grasses remain co-dominant with non-native annual species (Heady 1988;

Stromberg et al. 2001). European perennial grasses, however, are becoming increasingly common in the northern California coastal prairie, where they often form dense stands in which only a few native species co-exist (Peart 1989). The perennial grass invaders include species known to be strong competitors in their native range, for example the fast-growing *Holcus lanatus* L. and *Dactylis glomerata* L., which out-compete neighboring plants for nitrogen (N) (van der Werf et al. 1993), and *Festuca arundinacea* Schreber, which has strong competitive effects on neighbors even in stressful environments (Grime 1979).

The invasion of California coastal prairie by exotic perennial grasses may be facilitated by increased nitrogen (N) availability (Corbin and D'Antonio 2004). Increased N differentially favors non-native species over less N-responsive native species in a wide variety of ecosystems (e.g. Huenneke et al. 1990; Limpens et al. 2003; Lowe et al. 2003). Many coastal prairie sites experience anthropogenically elevated N levels: N deposition rates surrounding the San Francisco Bay Area can be as high as 10–15 kg N/ha/year (Weiss 1999). Soil N levels can also be increased by the invasion of N-fixing shrubs such as Scotch and French broom (*Cytisus scoparius* (L.) Link and *Genista monspessulana* (L.) L., respectively) or the native yellow bush lupine (*Lupinus arboreus* Sims.), and their subsequent removal *via* restoration or natural die-back (Maron and Connors 1996; Haubensak 2001).

Very little information exists on how increased soil N availability affects competition between native and exotic perennial grasses in coastal prairie. In a field experiment, Corbin and D'Antonio (2004) found that sawdust addition, a management strategy intended to decrease N availability, did not strongly alter competitive interactions. However, their sawdust additions did not have a consistent effect on N availability, so this does not rule out the possibility of altered competitive dynamics with increased N (Corbin and D'Antonio 2004). Several researchers have addressed N effects on competition between native perennial and exotic annual grasses in coastal prairie. For example, Maron and Connors (1996) documented higher cover of non-native annual grasses in areas where bush lupines had recently died from insect attack. A subsequent experimental study demonstrated greater growth of annual exotic grasses in patches of experimentally killed *Lupinus*, suggesting that a fertilization effect favored the fast-growing annuals (Maron and Connors 1996). Similarly, in a greenhouse experiment, high N conditions decreased the relative competitive ability of seedlings of the native perennial *Hordeum brachyantherum* Nevski against the annual exotic *Lolium multiflorum* Lam. (Kolb et al. 2002). It is possible that non-native perennial grasses are also more responsive to N-enrichment than native perennial grass species. Information about the fertilization responses of exotic vs. native perennial grasses when grown together could allow us to determine whether increased N availability facilitates the invasion of California coastal prairie.

We designed a greenhouse experiment to examine pairwise interactions between newly established native and exotic perennial grasses from the California coastal prairie, at two levels of soil N. Although offering somewhat limited conclusions, short-term greenhouse studies can be useful in developing a 'first cut' understanding of competitive interactions among a number of species (Gibson et al. 2003). Furthermore, the disturbed soil and freedom from adult competition in a greenhouse experiment mimic the conditions in soil disturbances created by fossorial rodents, a common feature of California grasslands (Peart 1989). Soil disturbances create openings in the dense perennial vegetation of native-dominated coastal prairie sites, thereby allowing the recruitment of new individuals in classic gap-dynamic fashion (Peart 1989; Kotanen 1997). Post-disturbance interactions often exert a controlling influence on which species can ultimately occupy new open space (Sousa 1984). Therefore, the ability of exotic perennial grasses to dominate small disturbances more quickly than native species could contribute to their invasion into surrounding coastal prairie. Similarly, the ability of some species to make use of fleeting windows of increased resource availability has been shown to contribute to invasion in other systems (Davis and Pelsor 2001).

To assess the competitive interactions among native and introduced perennial grasses in the California coastal prairie, we selected three common native perennial grass species and three of the region's most aggressive introduced perennial grasses. Although we do not have a large number of taxa within the categories of native and exotic

species, our study will allow us to evaluate whether there are consistent differences between them. We evaluated competition in terms of species' competitive effects on neighbors and their responses to competition (Goldberg and Werner 1983). In general, when exotic species have either strong competitive effect on neighbors or little response to them, it suggests that competitive ability may explain their spread into native-dominated vegetation (Hager 2004). We were also interested in determining if competitive effect and response were correlated among native and exotic species. Although such a correlation is not necessarily predicted by theory (Goldberg and Barton 1992), it occurs quite frequently (e.g. Roxburg and Wilson 2000; Freckleton and Watkinson 2001); when it does, it means that strong competitors have a double advantage over their subordinates. We also examined the competitive dynamics between individual pairs of species to determine whether each pair competed asymmetrically. We used that information to determine the hierarchy of relative competitive ability among the six species studied (Roxburgh and Wilson 2000; Freckleton and Watkinson 2001). The specific questions we addressed are: (1) What are the overall competitive effects, responses and hierarchy of the six species studied? (2) What species traits correlate with competitive dominance or suppression? (3) How does increased N availability affect competition between these species? (4) How does competitive ability vary among native and exotic species, i.e. are exotic species always better competitors than native ones, or is competitive rank species-specific?

Methods

The exotic species we studied were *Holcus lanatus*, *Phalaris aquatica* L., and *Festuca arundinacea*, and the natives were *Festuca rubra* L., *Agrostis oregonensis* Vasey and *Nassella pulchra* (A. Hitchc.) Barkworth (nomenclature here and elsewhere follows Hickman 1993). The California Invasive Plant Council lists the three exotic species we selected as being of conservation concern (Anderson et al. 1999). We collected seeds of all species at Tom's Point, a private nature preserve administered by Audubon Canyon Ranch, adjacent to Tomales Bay and about 60 km north of the Golden Gate (38°13′ N, 122°57′ W).

We sowed the seeds in a greenhouse at the University of California, Berkeley in September 1998. Seedlings were grown in 49 ml Fir Cell Cone-tainers^{TM} (Steuwe and Sons, Corvallis, Washington) filled with Davis Mix standard greenhouse soil. In February 1999 we transferred plants into 2-gallon plastic pots filled with sterilized University of California Mix standard greenhouse soil, a coarse-textured, low-nutrient mix (50% fine sand, 50% peat moss). At the time of transplanting we harvested, dried and weighed the shoots of 20 randomly-selected individuals per species to evaluate their biomass.

We arranged planted pots randomly on greenhouse benches and re-randomized them twice during the experiment to avoid bench location effects, so there are no block effects in our statistical design. We watered the pots every 3ôCPádays with automatic or hand-held sprinklers to maintain adequate moisture. Supplemental light was not provided because the greenhouse was well lit and unshaded, and the greenhouse was ventilated to keep it as cool as possible as the weather warmed. Light and temperature conditions in the greenhouse therefore mimic regional natural conditions as closely as possible.

Our treatments included singly-grown plants and every pairwise species combination (two plants per pot, planted 10 cm apart), repeated at two N levels. We replicated each treatment seven times. This design straddles two of the types defined by Gibson et al. (1999); it is a single-density diallel design, with the addition of singly-grown plants, allowing for the analysis of both intra- and interspecific competitive effects (Underwood 1986). For the fertilized treatment, we applied 5 g/m^2 N (blood meal) at the beginning of the experiment and after four months of growth, for a total N-addition of 10 g/m^2. To avoid P limitation, we applied 1 g/m^2 of inorganic P (triple phosphate) to all pots at the beginning of the experiment and after 4 months of growth, for a total P addition of 2 g/m^2. After 20 weeks of growth, we harvested and dried all plant shoots. Plant roots for singly-grown plants were harvested and washed in a 2 mm sieve; the roots of plants grown with a neighbor were too intertwined to separate, so we will not present root data for competition treatments.

For plants grown alone, we analyzed absolute shoot and root dry biomass and calculated root:shoot ratios. We used these measures of plant performance in the absence of a neighbor to evaluate differences among species in growth strategy that might help explain the results of the competition treatments (Freckleton and Watkinson 2001). We also used them to calculate a relative shoot yield per plant for plants grown in competition:

$$\text{RYP}_{ij} = \frac{Y_{ij}}{Y_i}$$

where Y_{ij} is the shoot mass of an individual of species i grown with a neighbor of species j, and Y_i is the mean shoot mass of species i grown alone. Since these values were calculated using the mean shoot biomass of singly-grown plants for each species at either high or low N, they control for species differences both in size and in innate response to fertilization.

Weigelt and Jolliffe (2003) call the index we calculated 'competitive response,' and distinguish it from the more general term 'relative yield' because it evaluates individual plant performance instead of performance per unit area. It is an index of competitive response when evaluated as a function of focal plant identity because it compares the size of plants grown with a neighbor to their potential size without one (Goldberg and Barton 1992). However, when the index is examined as a function of neighbor identity, it represents the competitive effect of that neighbor species, i.e. the degree to which it decreases the growth of its neighbor (Goldberg and Barton 1992). We use the index to evaluate both competitive response and effect, so we follow Roxburgh and Wilson (2000) in using the term relative yield per plant (RYP). Note that since RYP values represent the proportion of potential growth achieved by a plant grown in competition, they can appear counterintuitive. A large focal species RYP indicates that a species has small response to competition, since its growth was only slightly affected by the presence of a neighbor. Conversely, a large neighbor species RYP shows that a species has a small competitive effect on its neighbors, which therefore attain a large proportion of their potential shoot biomass.

In addition to evaluating overall competitive response and effect for each species, we compared the reciprocal RYP pairs for each interspecific species combination. Reciprocal RYP values were compared within each N-level, e.g. the RYP of a *Holcus* individual grown with *F. arundinacea* at high N vs. that of the *F. arundinacea* grown with that *Holcus*. Significantly different RYP values for the two species in a given pairing indicates that the species competed asymmetrically, i.e. one species decreased its neighbor's growth more than the other (Roxburgh and Wilson 2000; Weigelt and Jolliffe 2003). Information on the competitive asymmetry among a group of species can be used to arrange species into a competitive hierarchy, which reflects their theoretical relative competitive ability (Roxburgh and Wilson 2000; Freckleton and Watkinson 2001).

We analyzed the data using JMP IN® 3.2.6 (SAS Institute Inc., Cary, North Carolina). The absolute shoot and root biomass data and the RYP values were cube-root transformed to normalize distributions and equalize variances among experimental groups (Zar 1999). We present back-transformed values and asymmetrical 95% CI bars in the following figures, to facilitate the evaluation of significant differences among treatments; in Table 2 we present the raw RYP values for each pairwise comparison and their standard errors, to facilitate comparison with other studies.

We used two-way ANOVAS to evaluate species and fertilization effects on absolute shoot and root biomass of plants grown alone and on focal and neighbor species RYP values, and conducted *post hoc* means comparisons using Tukey tests ($\alpha = 0.05$). Data points for the analysis of focal and neighbor species RYP were randomly drawn from pots, stratified as one per pot and equal numbers across each of the species and N level treatment combinations. Thus, each pot is used only once in each analysis. The values in Figure 3 therefore differ slightly from the raw data presented in Table 2. To compare the reciprocal RYP values of the two plants grown in each competition pot, we determined the absolute value of their difference and compared that value to zero using a one-tailed *t*-test. A significant result means that the two RYP values were not identical, i.e. asymmetrical competition occurred: one species decreased the growth of the other more than its own growth was reduced. We used a Bonferoni-adjusted α of 0.002 to account for the 30 separate comparisons of reciprocal RYP values across all

species and N treatment combinations (Moore and McCabe 1999).

Results

Initial plant size

The six species differed in average shoot biomass at the time of transplanting ($F_{5,111} = 6.13$; $p < 0.001$). *F. arundinacea* had significantly greater shoot biomass than *F. rubra*, but none of the other pairwise comparisons were significant (Tukey tests, data not shown). Therefore, we concluded that the size differences at the time of transplanting are unlikely to introduce bias to our comparisons of species performance.

Singly-grown plants

Shoot biomass varied three-fold among the six species when they were grown alone, and N addition increased shoot weights by 86–107% (Table 1 and Figure 1). However, no significant interaction between species and N-level was observed. *Post hoc* comparisons of species differences, averaging over N level and comparing all six species to each other, indicate significant size differences only between the two largest species (*F. arundinacea* and *Agrostis*) and *Nassella* (Tukey tests; Figure 1).

The root biomass of singly-grown plants also differed significantly among species, and root biomass was increased by fertilization (Table 1 and Figure 2a). There was no interaction between species identity and fertilization. *Post hoc* comparisons of the main effect of species suggest that *Holcus* had the greatest overall root biomass and *Nassella* the least, with the other four species having similar, intermediate values (Tukey tests; Figure 2a). Species also differed in their root: shoot ratios (Table 1 and Figure 2b). Fertilization decreased biomass allocation to roots, but there was no interaction between species identity and N level (Table 1 and Figure 2b). Because it appeared that the pattern of decreased root allocation in response to fertilization was driven primarily by *Holcus*, we used *t*-tests to compared the root: shoot ratio of fertilized and unfertilized plants within each species. R:S ratio was significantly greater in control plants than fertilized ones for *Holcus* and *F. arundinacea* ($t_{11} = 2.24$ and $t_{11} = 2.46$, respectively; $p < 0.05$) but not for other species. *Post hoc* comparisons of the six species (averaging over the two N-levels within each) revealed two distinct groups, with *Holcus* having the highest root:shoot ratio and all other species having similar root:shoot ratios (Tukey tests; Figure 2b).

Plants grown with a neighbor

Using the mean shoot biomass of singly-grown plants for each species and N treatment combination (Figure 1), we calculated the RYP for each individual grown with a neighbor (Table 2). Focal

Table 1. Significance of experimental treatments on the biomass of singly-grown plants and the RYP for plants grown with a neighbor, as shown in Figures 1–3.

	Err. df	Species (df = 5)		N level (df = 1)		Species*N level (df = 5)	
		F	P	F	P	F	P
Singly-grown plants							
Shoot biomass	72	9.1	<0.001	106.6	<0.001	0.1	0.984
Root biomass	67	26.8	<0.001	18.7	<0.001	1.2	0.327
Root:shoot ratio	67	26.2	<0.001	6.9	<0.02	1.6	0.181
Plants with a neighbor							
Focal RYP	276	13.0	<0.001	2.63	0.106	0.55	0.740
Neighbor RYP	276	23.4	<0.001	2.56	0.111	0.36	0.876

Plants were randomly selected for inclusion in the analysis of plants grown with a neighbor, stratified to one per pot and equal numbers across species and N treatment combinations.
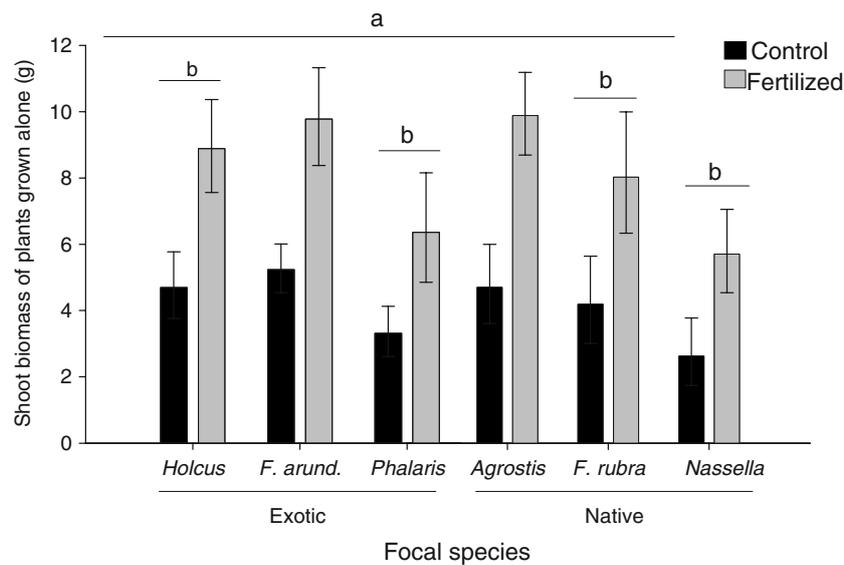
Figure 1. Shoot biomass of plants grown alone, for control vs. N-fertilized plants (mean ± 95%CI). Shoot biomass was significantly different among species, and fertilization caused a significant increase in shoot biomass in all species (results from ANOVA). Letters indicate species that were not significantly different in *post hoc* tests averaging over N-level (Tukey tests).

plant RYP, representing the competitive response of each species to the presence of a neighbor, differed significantly across species (Table 1 and Figure 3a). Fertilization did not affect competitive response (Table 1 and Figure 3a). *Post hoc* comparisons of species' means indicate that only *Holcus* (the species with the least response to the presence of a neighbor) and *Nassella* (the species with the greatest) differed significantly in RYP (Tukey tests; Figure 3a). Neighbor plant RYP, or competitive effect, also differed across species (Table 1 and Figure 3b). There was no effect of fertilization on neighbor plant RYP. *Post hoc* comparisons revealed that when *Holcus* was the neighbor, RYP was significantly smaller than when plants were grown with any other species. Plants with *Phalaris*, *F. arundinacea*, or *Agrostis* neighbors formed an intermediate group, and plants grown with the native species *F. rubra* and *Nassella* had significantly larger RYP than plants grown with other species (Tukey tests; Figure 3b). Overall neighbor and focal plant RYP were significantly negatively correlated ($r = -0.955$, $p < 0.003$) across species.

T-tests comparing the absolute value of the difference in RYP of plants grown together to zero indicated that the difference in RYP was significantly different from zero in 14 of 30 reciprocal pairs (bold values in Table 3). In these cases, asymmet-

rical competition occurred, so that one species decreased the growth of the other more than its own growth was reduced. Reciprocal RYP values differed significantly at one N-level but not at the other for four species combinations, marked with an asterisk in Table 3. The pattern of asymmetrical interactions was more or less transitive, allowing species to be organized in a linear competitive hierarchy. *Holcus* was competitively superior to all species under at least one N treatment (it had symmetrical competition with *F. arundinacea* and *Phalaris* under fertilized and control conditions, respectively). *F. arundinacea* was the second most dominant species, out-competing *F. rubra* and *Nassella* under both control and fertilized conditions. *F. arundinacea*, *Phalaris*, and *Agrostis* were equivalent competitors, since their reciprocal RYP values never differed significantly. *Phalaris* out-competed *Nassella* when fertilized, and *F. rubra* out-competed *Nassella* under control conditions.

Discussion

Competitive responses and effects

Our results do not support the idea that exotic perennial grasses in California's coastal prairie grasslands have consistently greater competitive
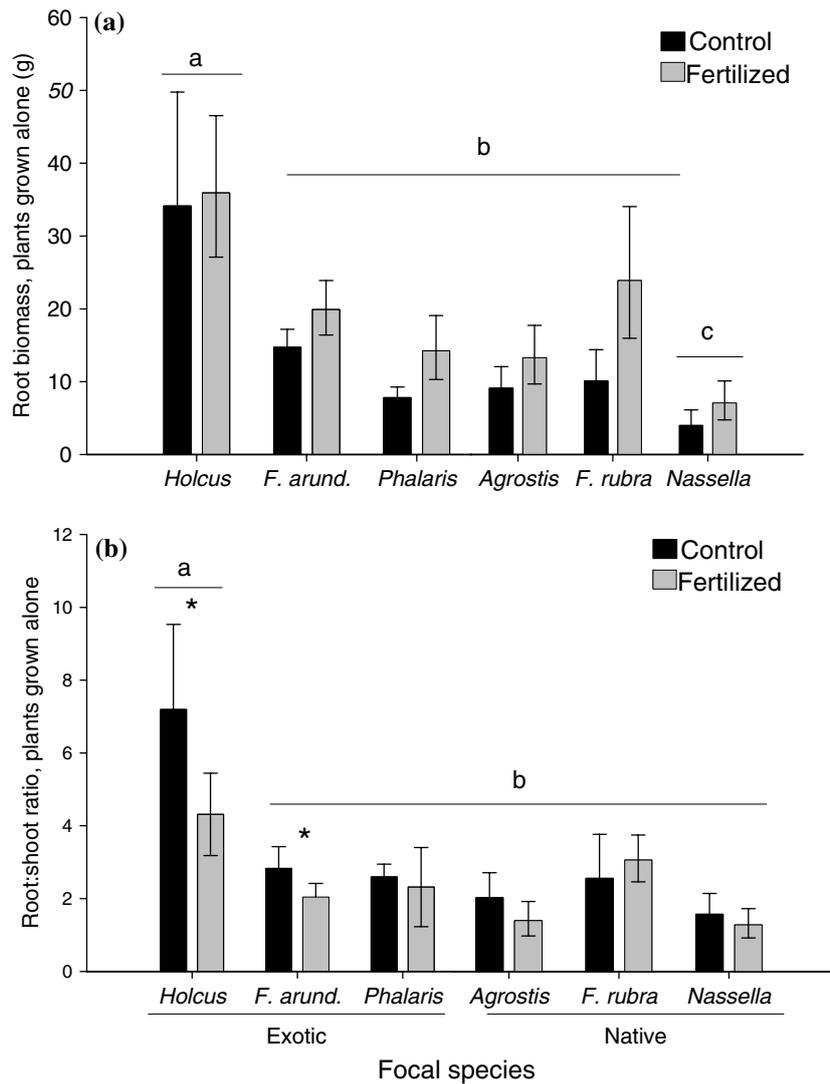
Figure 2. Root biomass (a) and root:shoot ratio (b) of plants grown alone, for control vs. N-fertilized plants (mean ± 95%CI). The main effects of species and N-level were significant for both analyses, but their interactions were not (results from ANOVA). Letters indicate origin groups or species that were not significantly different in *post hoc* tests averaging over N-level (Tukey tests). Stars indicate species in which fertilized and control plants had significantly different root:shoot ratios (*t*-tests).

abilities than do native bunchgrasses. Instead, we found a continuum in species' competitive response and effect abilities that crossed the categories of native and exotic species, so that most species did not differ in pairwise tests of mean RYP. Two exceptions are the exotic grass *Holcus* and the native species *Nassella*. *Holcus* had significantly greater focal plant RYP than *Nassella*, meaning that *Nassella* was more suppressed by the presence of a neighbor than *Holcus* (Figure 3a).

Likewise, *Holcus* had a significantly smaller neighbor RYP than any other species we studied, meaning that it had the greatest effect on its neighbors, while the group *F. rubra*/*Nassella* had the least (Figure 3b). Similar to the results for overall competitive response and effect, reciprocal RYP values showed that *Holcus* was a superior competitor to all other species except *F. arundinacea* and *Phalaris* at high and low N, respectively. All species except *Agrostis* were competitively

Table 2. Raw data for mean RYP and SE (in parentheses) for each species combination; the first value in each pair is for controls and the second for fertilized pots.

Focal	Neighbor						Mean response
	Holcus	F. arundinacea	Phalaris	Agrostis	F. rubra	Nassella	
Holcus	0.55/0.45 (0.05/0.04)	0.75/0.63 (0.05/0.06)	0.89/0.84 (0.09/0.09)	0.84/0.78 (0.07/0.09)	10.0/0.97 (0.04/0.06)	0.94/0.86 (0.06/0.06)	**0.78/0.71 (0.03/0.04)**
F. arundinacea	0.51/0.41 (0.05/0.05)	0.56/0.54 (0.03/0.03)	0.65/0.52 (0.07/0.06)	0.55/0.59 (0.09/0.07)	0.65/0.93 (0.09/0.09)	0.94/0.88 (0.07/0.07)	**0.63/0.63 (0.03/0.04)**
Phalaris	0.52/0.29 (0.18/0.02)	0.47/0.49 (0.09/0.04)	0.53/0.54 (0.07 /0.05)	0.61/0.42 (0.08/0.04)	0.90/0.85 (0.17/0.13)	0.78/0.88 (0.12 /0.05)	**0.62/0.57 (0.05/0.04)**
Agrostis	0.27/0.29 (0.03/0.04)	0.46/0.43 (0.04/0.08)	0.45/0.57 (0.09/0.05)	0.70/0.44 (0.06/0.04)	0.92/0.62 (0.14/0.08)	0.88/0.83 (0.05/0.08)	**0.62/0.54 (0.04/0.03)**
F. rubra	0.22/0.27 (0.03/0.03)	0.45/0.38 (0.04/0.03)	0.45/0.35 (0.06/0.08)	0.41/0.51 (0.11/0.08)	0.69/0.60 (0.08/0.05)	0.65/0.77 (0.06/0.12)	**0.51/0.48 (0.04/0.04)**
Nassella	0.31/0.17 (0.14/0.02)	0.38/0.22 (0.07/0.03)	0.29/0.24 (0.04/0.03)	0.34/0.24 (0.03/0.07)	0.40/0.54 (0.04/0.07)	0.62/0.53 (0.05/0.03)	**0.42/0.36 (0.03/0.03)**
Mean effect	**0.42/0.34 (0.04/0.02)**	**0.52/0.47 (0.02/0.03)**	**0.53/0.52 (0.04/0.04)**	**0.59/0.50 (0.04/0.03)**	**0.75/0.74 (0.05/0.04)**	**0.77/0.74 (0.03/0.03)**	

Each value in the table represents the mean RYP of seven replicates per species combination under control or fertilized conditions. Reading down a column reveals the competitive effect of each species on its various neighbors; reading across a row indicates the competitive response of a given species to the presence of each neighbor species. The final column and bottom row give the mean competitive response and effect, respectively, for each focal and neighbor species. Note that the values here are different from those analyzed in Table 1 because we re-sampled our data to use the results from each pot only once in our analyses of mean RYP values (see Methods).

superior to *Nassella* under at least one N condition (Table 3).

Thus, any competitive superiority of exotic species over the native plants studied was driven primarily by *Holcus* and *Nassella*. These findings support the general assertion that *a priori* grouping of co-occuring species into the categories 'native' and 'exotic' can mask underlying similarities between and variation within those categories (Levine and D'Antonio 1999; Davis et al. 2001). Species-level differences in relative growth rate, allocation or phenology are more likely to provide information about relative competitive ability than is geographic origin (Levine and D'Antonio 1999; Davis et al. 2001).

What species-level trait differences contributed to *Holcus*'s competitive strength and *Nassella*'s relative weakness? One way in which these species differed from the other grasses studied is in their root production. Although a number of factors can lead to a lack of correspondence between root biomass and belowground competitive ability (Casper and Jackson 1997), allocation to roots has often been correlated with overall competitive dominance in perennial species (e.g. Gurevitch et al. 1990; Aerts et al. 1991) and with species rank in pairwise competition experiments similar to our own (e.g. Freckleton and Watkinson 2001; Hager 2004). When grown alone, *Holcus* had significantly greater root biomass and root:shoot ratio than any other species in the experiment, while *Nassella* had significantly less root biomass and significantly lower root:shoot ratio than did *Holcus* (Figure 2b). If root traits in competition treatments followed a similar pattern, the competitive rankings of *Holcus* and *Nassella* may have reflected their ability to compete for soil resources.

We believe that initial growth rates also help explain the competitive rankings of *Holcus* and *Nassella* in this experiment. Maximum relative growth rate and seed characteristics (which can affect seedling growth rate) are frequent correlates of relative competitive ability (reviewed in Goldberg 1996; Freckleton and Watkinson 2001). In our experiment, *Holcus*'s estimated growth rate during the first 5 weeks was significantly greater than that of any other species, while that of *Nassella* was significantly smaller (growth rates calculated using allometric relationships between final shoot biomass and plant height and basal diameter; data not shown). Growth rates of all
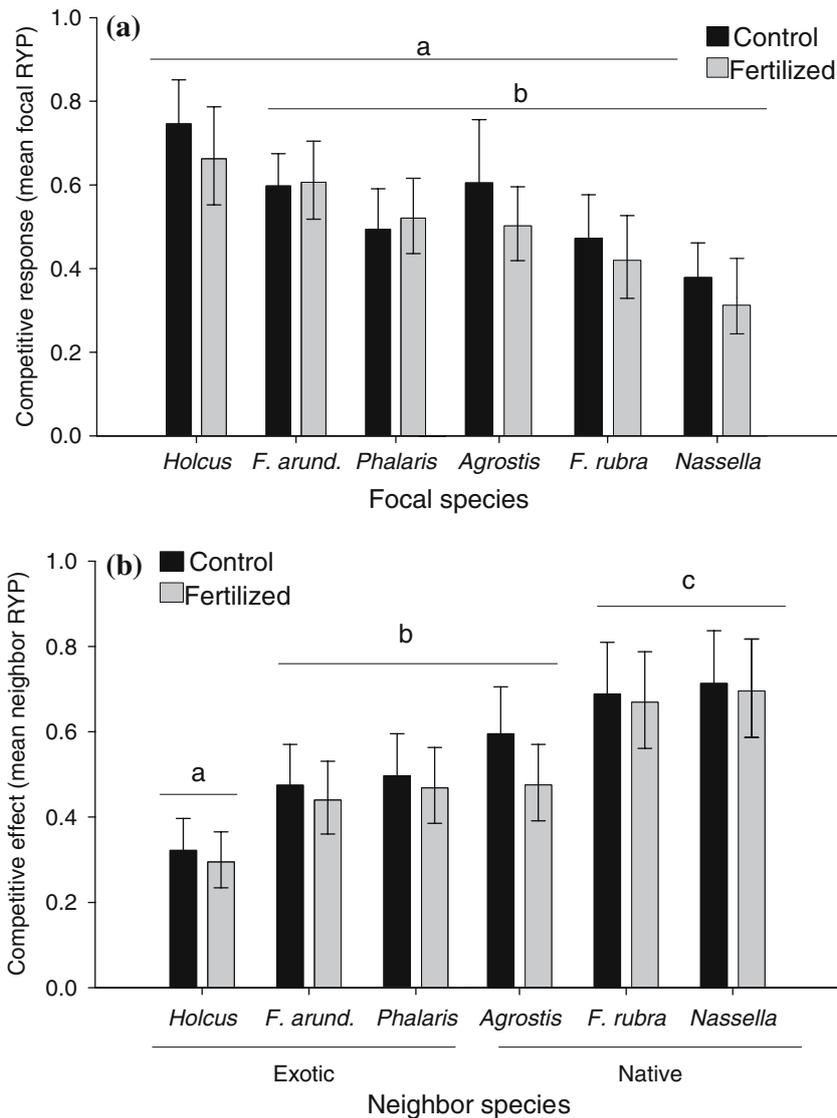
Figure 3. Mean RYP of plants grown with a neighbor, for control vs. N-fertilized plants (mean ± 95% CI). (a) Competitive responses of focal species. (b) Competitive effects of neighbor species. For both comparisons, species was significant but N-level was not (results from ANOVA). Within each graph, letters indicate origin groups or species that were not significantly different in *post hoc* tests (Tukey tests). Individuals were randomly selected for RYP analyses, stratified to one per pot and equal numbers across each species and N level treatment combination, so the values presented here do not match those in Table 2.

species were much lower later in the experiment (data not shown). It appears that species' competitive rankings were set early on, so that initial growth rates were a critical component of competitive ability in the experiment.

Aboveground shoot biomass, another common correlate of relative competitive ability (Goldberg 1996; Keddy et al. 2002), did not explain patterns

of competitive dominance and subordination in our experiment. Despite their very different performance in the presence of a neighbor, the aboveground biomass of singly-grown *Holcus* and *Nassella* were indistinguishable from one another (Figure 1). Furthermore, *F. arundinacea* and *Agrostis*, which were out-competed by *Holcus* under control or both N conditions, respectively

Table 3. Matrix of *t*-statistics and their significance levels from one-tailed *t*-tests of reciprocal RYP values for each competition treatment.

	F. arundinacea	Phalaris	Agrostis	F. rubra	Nassella
Holcus	$t_6=5.3/t_5=3.3$ **0.001**/0.011*	$t_4=4.1/t_6=5.3$ 0.007/**0.001***	$t_6=5.4/t_5=6.7$ **0.001/0.001**	$t_6=16.2/t_2=12.3$ **0.001/0.001**	$t_6=5.9$, $t_6=8.6$ **0.001/0.001**
F. arundinacea		$t_3=2.8/t_5=3.5$ 0.350/0.009	$t_4=4.4/t_5=3.4$ 0.011/0.010	$t_6=3.0/t_6=4.8$ **0.001/0.001**	$t_6=5.1/t_5=8.5$ **0.001/0.001**
Phalaris			$t_9=2.6/t_6=4.4$ 0.014/0.003	$t_6=2.2/t_5=2.6$ 0.033/0.025	$t_6=3.7/t_6=11.2$ 0.005/**0.001***
Agrostis				$t_5=2.9/t_6=3.0$ 0.016/0.012	$t_5=2.6/t_5=3.4$ 0.024/0.010
F. rubra					$t_6=5.1/t_4=3.0$ **0.001**/0.021*

The first value in each pair is for controls and the second for fertilized plants. We determined the absolute value of the difference in RYP between the two plants in each pot, and then calculated a mean difference for each species and N level treatment combination. This value was compared to zero, using a Bonferroni-adjusted $\alpha = 0.002$ to account for multiple comparisons. Significant *p*-values (bold typeface) indicate that competition between those species is asymmetric. Asterisks (*) mark species combinations in which competition was asymmetric at one N-level but not the other.

(Table 3), had a trend towards greater shoot biomass than *Holcus* when grown alone (Figure 1). Apparently, species traits relating to performance in the presence of a neighbor drove patterns in relative competitive ability in our experiment, rather than potential performance when grown alone.

Nitrogen effects on competition

In a number of ecosystems worldwide, natural and anthropogenic increases in N availability have been shown to increase the success of fast-growing, N-responsive species, in some cases resulting in the greater dominance of invasive exotic species (Huenneke et al. 1990; Maron and Connors 1996; Barger et al. 2003; Lowe et al. 2003). In this study, we found that two of the exotic species studied significantly decreased their root:shoot ratio in response to fertilization (*Holcus* and *F. arundinacea*; Figure 2b). Species with this trait are predicted to disproportionately reduce the growth of less plastic neighbors under high-N conditions (e.g. Grime et al. 1991), although Reynolds and D'Antonio (1996) did not find the relationship consistent across studies. In our experiment, fertilization had no effect on RYP for plants grown with a neighbor. Thus, N availability had no effect on species' responses to or effects on neighbors, once innate responses had been actored out (Figure 3a, b). Examining the competition between individual species rather than the overall patterns in RYP did not provide any additional evidence for the effect of N availability on species interactions: fertilization caused the competition between only two pairs of species to switch from symmetric to asymmetric (*Holcus–Phalaris* and *Phalaris–Nassella*), while an equal number of species pairs competed asymmetrically at low but not at high N (*Holcus–F. arund.* and *F. rubra–Nassella*; Table 3).

Thus, we have no evidence that short-term N-enrichment is a major influence on the invasion of exotic perennial grasses in California coastal prairie. This suggests that decreasing N availability may not be a critical step towards the successful restoration of the habitat (Corbin and D'Antonio 2004). We did, however, observe a trend for increased strength of competition at high N (plants attained a smaller fraction of their potential shoot biomass when fertilized, Figure 3a). Given the short timeframe of the experiment, it remains possible that the trend could intensify with time, as exotic plants develop larger root systems and more thoroughly exploit nutrient pools, to the detriment of native species. Furthermore, small changes in the strength of competition could interact with other factors, such as disease or herbivory, that might negatively affect native relative to exotic species.

In many of the studies that have demonstrated a significant effect of N addition on competition between native and exotic species under controlled

conditions, the species representing the two origin groups differ more strikingly than they do in this system; examples include perennial vs. annual grasses (Kolb et al. 2002; Lowe et al. 2003), *Sphagnum* moss vs. angiosperm shrubs (Limpens et al. 2003), and herbaceous grassland species vs. trees (Siemann and Rogers 2003) (although Carino and Daehler (2002) and Barger et al. (2003) did find that nutrient additions altered competition between native and exotic perennial C_4 grasses). The similarity of native and exotic perennial grass growth responses to N in our study, and the resultant lack of N effect on competition, raises the possibility that the enhancement of invasion with N enrichment may be less likely in systems where the native and exotic species have a similar growth form, phenology, or nutrient acquisition strategy.

Implications

While the short time frame and greenhouse conditions of our experiment may limit our ability to generalize, our results are similar to those of a field experiment using the same initial source of seedlings (Corbin and D'Antonio unpublished data), adding to our confidence in their applicability. In the field experiment, equal-density plots were established of the native species alone, the exotic species alone, and the native and exotic species grown together in equal proportion. For the first 3 years, results from the field experiment reinforce the major patterns we observed: exotic plants had a greater effect on neighbors than did native ones, and *Agrostis* was the native species with the smallest response to competition from exotic species.

Holcus also had the greatest shoot biomass production of any species during the first year of the field experiment; however, its aboveground biomass production declined in the second and third years, probably in response to competition from *Phalaris* and *F. arundinacea* (Corbin and D'Antonio unpublished data). Grime (1979) characterized *Holcus lanatus* as a 'ruderal-perennial herb,' a group with the capacity for rapid vegetative growth into open areas and a competitive disadvantage against taller perennials that form densely-packed stands; *F. arundinacea* and *Phalaris* both grow in this way (personal observation).

Holcus's fast growth and competitive dominance in this and several other greenhouse experiments (van der Werf et al. 1993; Schippers et al. 1999; Roxburgh and Wilson 2000) may reveal the 'gap-filling' abilities of the species, but not its longer-term competitive dynamics with other perennial species.

Despite the possibility that *Holcus* does not compete well against other perennial grasses in the long-term, we believe that it deserves greater management attention. *Holcus*'s strong competitive abilities against native species at the seedling stage in this study means that it may successfully dominate the open spaces created by mammalian disturbance, which represent an important regeneration niche for native grasses in coastal prairie (Peart 1989). Similarly, the restoration of native grasses from seed may not be possible if *Holcus* is present, unless native seedlings are protected from its competitive effects. This might be accomplished by depleting the *Holcus* seedbank prior to planting.

Our finding that *Nassella* did poorly in response to competition was also observed in the field experiment, where it had the lowest aboveground productivity of the six species studied (Corbin and D'Antonio unpublished data). *Nassella* was long considered to have been the dominant species in pre-invasion California grasslands (Heady 1988; Hamilton 1997). As a result, it is often the focus of restoration projects and used as an 'indicator species' for determining community responses to management strategies (Hatch et al. 1999). However, recent work has challenged the assumption that *Nassella* was a dominant species throughout its range (Hamilton 1997; Holstein 2001); instead, population-level variation may have allowed it to match, with varying levels of success, the broad range of conditions found across the state (Huntsinger et al. 1996). The poor competitive ability of *Nassella* in our study supports the idea that it was not a dominant species in coastal prairie, although it is possible that the short timeframe of our experiment underestimates *Nassella*'s long-term competitive ability. We recommend against a focus on *Nassella* in coastal prairie restoration projects, however, since its seedlings may not perform well in competition with exotic perennial grasses, particularly *Holcus*. As this work also shows, other native species (especially *Agrostis*) may be better

able to establish despite strong competition from invasive perennial species.

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