Oecologia (2008) 155:357–366
DOI 10.1007/s00442-007-0909-6

COMMUNITY ECOLOGY - ORIGINAL PAPER

Abiotic constraints on the competitive ability of exotic and native grasses in a Pacific Northwest prairie

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Received: 11 July 2006 / Accepted: 18 October 2007 / Published online: 21 November 2007

Abstract In prairie ecosystems, abiotic constraints on competition can structure plant communities; however, the extent to which competition between native and exotic plant species is constrained by environmental factors is still debated. The objective of our study was to use paired field and greenhouse experiments to evaluate the competitive dynamics between two native (*Danthonia californica* and *Deschampsia cespitosa*) and two exotic (*Schedonorus arundinaceus* and *Lolium multiflorum*) grass species under varying nutrient and moisture conditions in an upland prairie in the Willamette Valley, Oregon. We hypothesized the two invasive, exotic grasses would be more competitive under high-nutrient, moderate-moisture conditions, resulting in the displacement of native grasses from these environments. In the field, the experimental reduction of competition resulted in shorter, wider plants, but only the annual grass, *Lolium multiflorum*, produced more aboveground biomass when competition was reduced. In the greenhouse, the two exotic grasses produced more total biomass than the two native grasses. Competitive hierarchies were influenced by nutrient and/or moisture treatments for the two exotic grasses, but not for the two native grasses. *L. multiflorum* dominated competitive interactions with all other grasses across treatments. In general, *S. arundinaceus* dominated when in competition with native grasses, and *D. cespitosa* produced the most biomass in monoculture or under interspecific competition with the other native grass, *D. californica*. *D. californica*, *D. cespitosa*, and *S. arundinaceus* all produced more biomass in high-moisture, high-nutrient environments, and *D. cespitosa, L. multiflorum*, and *S. arundinaceus* allocated more biomass belowground in the low nutrient treatment. Taken together, these experiments suggest the competitive superiority of the exotic grasses, especially *L. multiflorum*, but, contrary to our hypothesis, the native grasses were not preferentially excluded from nutrient-rich, moderately wet environments.

Keywords Competition · Invasive species · Moisture availability · Nutrients · Willamette Valley

Introduction

Invasion by exotic species is recognized as a leading threat to native biodiversity and ecosystem functioning (Vitousek et al. 1997; Mack and D'Antonio 1998; Chapin et al. 2000). In prairie ecosystems, invasive species have been identified as a primary obstacle to successful restoration, and this has been attributed to their ability to competitively exclude native species (Ewing 2002). In particular, theory suggests that invasive species are competitively superior in high-quality habitats (i.e., high-nutrient and mesic-moisture conditions), forcing native species to take "refuge" in low-quality habitats (Hoopes and Hall 2002; Lowe et al. 2003). However, empirical evidence to support this theory has been equivocal. Understanding how competition between native and exotic species interacts with abiotic factors to structure plant communities will be important for the conservation of native prairies.

Communicated by Jon Keeley.

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Multiple studies have stressed the dependence of competition upon environmental conditions such as water, light, and nutrient availability (e.g., Lowe et al. 2003; Suding et al. 2004a, 2004b; Kluse and Allen Diaz 2005). However, results vary regarding how abiotic factors affect the ability of exotic species to competitively exclude native species. A variety of mechanisms can explain why the population sizes of native and exotic grasses may be negatively correlated (Parker et al. 1993). In some cases, native species are able to survive in stressful, low-nutrient environments, but are out-competed by aggressive exotics under high-resource conditions (Huenneke et al. 1990; Maron and Connors 1996; Vinton and Burke 1997; Hamilton et al. 1999). For example, fertilization treatments that promoted growth in *Festuca idahoensis*, a perennial grass native to Pacific Northwest prairies, also facilitated success among aggressive exotic species, thereby reducing the positive effects on *F. idahoensis* (Ewing 2002). Similarly, some native perennial forbs and grasses in northern California were out-competed and replaced by exotic annual grasses in high-nutrient environments, but were able to persist in low-quality habitats (Murphy and Ehrlich 1986). In contrast, other studies show no effect of abiotic factors on competitive hierarchies between native and invasive plants. In northern California, the reduction of available nitrogen did not decrease the competitive suppression of native perennial bunchgrasses by exotic perennial and annual grasses over the course of two years (Corbin and D'Antonio 2004). Furthermore, water availability had no effect on the competitive outcome between a native and exotic grass in Canada (Bakker and Wilson 2001).

In previous research we observed large differences in the relative abundances of native and exotic plants in a remnant upland prairie in the Willamette Valley, Oregon (L. Pfeifer-Meister et al., manuscript in preparation). In a multiple regression analysis, soil moisture and inorganic nitrogen availability explained 63% of the variation in the proportion of native to exotic species biomass ($p = 0.003$). Areas with a high proportion of native biomass were wet and had low nitrogen availability, whereas a higher proportion of exotics were found in drier, nutrient-rich sites. We hypothesized that native species were restricted to these low-quality (nutrient-poor and wet) sites due to competitive exclusion by exotic species. Therefore, the objective of our study was to test the competitive dynamics among four grass species under varying nutrient and moisture conditions. We examined two native perennial grasses, *Danthonia californica* and *Deschampsia cespitosa*, and two common exotics, *Schedonorus arundinaceus* and *Lolium multiflorum*. We hypothesized that competitive hierarchies would change depending on abiotic conditions. Specifically, we predicted that the two invasive, exotic grasses would have greater competitive ability at high-nutrient, moderate-moisture conditions, resulting in the displacement of native species from these environments. We performed a paired study of field and greenhouse experiments to test our hypotheses. In the field competition experiment, we examined the effects of aboveground competition, inferred from the removal of neighbors, on established juvenile plants in four areas in a remnant upland prairie. However, within this prairie, soil moisture, nutrient availability, and other environmental variables covaried in complicated ways, so that it was difficult to determine how abiotic factors affected competitive hierarchies in the field. Hence, we also performed a greenhouse experiment in which we experimentally manipulated nutrients and moisture and examined the response of each species in monoculture and interspecific competition trials.

Materials and methods

Site description

We conducted the field component of the study on Mt. Pisgah, a small mountain located within Lane County's Howard Buford's Recreation Area, approximately 11 km from Eugene, Oregon. Mt. Pisgah is vegetated primarily by oak savannah and upland prairie interspersed with Douglas fir (*Pseudotsuga menziesii*) infill. Four 9 m × 5 m blocks were randomly located at approximately 190-m elevation in an upland prairie across a 6.1-ha area on a south-facing hill-slope at the base of the 467-m high Mt. Pisgah. Across the site, soil attributes varied considerably. Soil depth ranged from 8 to 106 cm with a mean of 43 cm, percent clay ranged from 42 to 68 with a mean of 57%, total percent carbon ranged from 1.8 to 5.2 with a mean of 3.4%, and pH ranged from 5.6 to 7.1 with a mean of 6.5 (for soil methods see Pfeifer-Meister and Bridgham 2007).

The Willamette Valley is characterized by a Mediterranean climate with wet winters and mild, dry summers. Over the past 30 years, the mean annual daily maximum and minimum temperatures were 17.2 and 5.0 °C, respectively, and mean annual precipitation was 117 cm (National Climatic Data Center 2005).

Species description

Danthonia californica Boland. is a tufted, native perennial bunchgrass (Pojar and MacKinnon 1994). Culms grow 30–100 cm tall, bearing 2–5 spikelets on average (Hitchcock 1971). This species is commonly found from low to high elevations across a continuum of wet to dry prairie (Pojar and MacKinnon 1994), ranging from California to British Columbia along the west coast of North America (Hitchcock 1971).

Deschampsia cespitosa L. is a densely tufted, native perennial bunchgrass with 20–120-cm-tall culms. This grass is found commonly from sea level to alpine elevations spanning a wet to dry prairie continuum (Pojar and MacKinnon 1994), although it is more common in wet environments. Within wetland habitats, *D. cespitosa* is found along the west coast of North America, as well as the northeastern United States (Hitchcock 1971).

Lolium multiflorum Lam. is a winter annual that germinates in the fall and generally flowers and produces seed the following spring (Pojar and MacKinnon 1994). Introduced from Europe, this species is grown extensively for commercial seed production, and its harvestable area covers over 47,000 ha of the Willamette Valley (Young 2005). *L. multiflorum* has spread across low-elevation habitats in the Willamette Valley (Pojar and MacKinnon 1994), and its range extends along the west coast of North America (Hitchcock 1971). *L. multiflorum* culms can grow to 100 cm tall and typically have 10–20 spikelets per stalk (Hitchcock 1971). The earliest specimen at the Oregon State University Herbarium that documented the occurrence of *L. multiflorum* in the Willamette Valley was from 1884.

Schedonorus arundinaceus (Schreb.) Dumort., formerly *Festuca arundinacea* or *Lolium arundinaceum*, is an exotic perennial introduced from Europe for agricultural purposes (Pojar and MacKinnon 1994). The area occupied by cultivated fields of *S. arundinaceus* has increased from 4,000 ha in 1979 to over 57,000 ha in 2003 (Young 2005). *S. arundinaceus* is abundant in low- to mid-elevation habitats, frequently colonizing fields, meadows, roadsides, or other disturbed areas (Pojar and MacKinnon 1994), with a range that extends along the west and east coasts of North America (Hitchcock 1971). *S. arundinaceus* is a tufted grass with flat, wide leaves and culms 50–100 cm tall (Pojar and MacKinnon 1994). The earliest specimen at the Oregon State University Herbarium that documented this Eurasian grass in the Willamette Valley was from 1918.

Field competition experiment

Our initial design called for experimental manipulation of competition on 12 naturally occurring juveniles of each grass species per 9 m × 5 m block. However, blocks were chosen randomly, and *D. cespitosa, L. multiflorum*, and *S. arundinaceus* juveniles were only found in two of the four blocks ($n = 24$), and *D. californica* juveniles were located in all blocks ($n = 48$). Substitute grass species were not available that occurred in all four blocks, and we decided to accept uneven occurrence of species in blocks rather than bias block selection.

A wire mesh ring, 5 cm in height and 23 cm in diameter, encircled each juvenile target plant. Juvenile individuals were classified by a small size (2–5 cm tall) and a small number (1–3) of emergent shoots. We established three levels of aboveground competition by clipping all vegetation surrounding the target individual within the ring for 100% competition reduction, clipping two diagonally oriented quarter sections for 50% competition reduction, and not clipping for 0% competition reduction. Clipping commenced on March 13, 2004 at the beginning of the growing season and was maintained every week until each species reached peak standing biomass. At the end of the experiment, length, width, and vegetative height of each target plant was measured in situ to evaluate growth morphology. Length was the longest horizontal dimension of the plant, while width was the horizontal distance perpendicular to the length. *L. multiflorum*, the only non-perennial in the study, produces reproductive stalks exclusively. Thus, in analyses of basal area:height ratio, we used the reproductive height for *L. multiflorum* while using vegetative height for all other species. In addition to measurements of plant morphology, each target plant was also clipped at the base and dried at 60°C for 48 h. We harvested *D. californica* on May 31, *S. arundinaceus* and *L. multiflorum* on June 9, and *D. cespitosa* on June 16, 2004, the date at which each species reached peak standing biomass. We weighed the dry aboveground biomass of each plant and separated out the seeds produced. Seeds were cleaned and counted by hand or by using a Pfeuffer Contador seed counter (Kitzigen, Germany).

To evaluate significant effects of competition on aboveground biomass and basal area:height ratio, we analyzed data from each species separately using a two-way ANOVA with competition as a fixed main effect and block as a random main effect. As seed count was highly correlated with aboveground biomass ($r = 0.92$), only biomass data is presented, but similar trends were observed for both variables. We log-transformed all data to normalize the distribution of residuals and used Tukey's pairwise comparisons to evaluate significant differences among competition levels within a species. All statistical analyses were performed using SPSS 11.0 for Windows.

Greenhouse competition experiment

In the greenhouse, we examined the growth of each grass species in monoculture and in all combinations of pairwise competition. These competition treatments were crossed with three levels of soil moisture and two levels of soil nutrient availability that were representative of field conditions. Each treatment contained four replicate pots. We obtained seeds from local suppliers of native plants or from fields near the location of the study site. Seeds obtained commercially represented genotypes from local prairies within the southern Willamette Valley. The seeds were cold-treated at 5°C for 30 days and then germinated at 20°C for ten days in Petri dishes wetted with gibberellic acid solution (1,000 mg/L) to ensure greater germination success and similar germination dates (Atwater 1980; Roy et al. 1999). We used fine-grain sand for the soil substrate, and placed four germinated seeds 5 cm away from their nearest neighbor in a square formation. Seeds were planted in circular pots 16.5 cm in diameter and 18 cm deep. Monoculture pots included four plants of the same species. Interspecific competition pots contained two plants of a given species on opposite corners of the competition square and two plants of another species in the remaining corners.

Each competition treatment was crossed with two levels of nutrient availability and three levels of moisture, representing a continuum from wet to dry prairie. In the high-moisture treatment, we placed pots in slightly larger containers and maintained the water level at 2.5 cm below the soil surface. Water was replaced bi-weekly. In the medium moisture treatment, we watered pots to field capacity every other day. To allow establishment of seedlings, we initially maintained plants in the low-moisture treatment in the same manner as plants in the medium-moisture treatment. Eight weeks into the experiment we reduced the frequency of water applications to twice a week in the low-moisture treatment pots. We established the water schedule by a visual examination of wilting in the plants. Our goal was to induce water stress without causing high mortality. All water added was deionized.

We based the low-nutrient treatment upon calculations of in situ nutrient uptake into vegetation in the portion of the remnant prairie with the lowest nutrient availability and lowest productivity, while the high-nutrient treatment was ten times that concentration. In the low-nutrient treatment, we added 50 mg N and 3 mg P per pot in the form of NH_4NO_3 and Na_2HPO_4, respectively. We added potassium, calcium, magnesium, and trace nutrients in equal amounts to all treatments based on ratios dictated by standard Hoagland's solution (Hoagland and Arnon 1938), so that plants were limited only by nitrogen and phosphorus. Nutrients were added weekly in 100-mL aliquots of solution with deionized water.

The greenhouse was unheated, but was cooled when the temperature rose above 33°C, and so the temperatures varied between 4.4 and 35°C, conditions typical of the growing season within the Willamette Valley (National Climatic Data Center 2005). The light system simulated a 16-h photoperiod. All pots were randomly assigned positions in the greenhouse and were moved biweekly so that environmental variation and shading by neighboring plants was randomized. The experiment spanned 90 days. At the end of the experiment, plants were harvested by separating the above- and belowground biomass for each species. The biomass was dried for 48 h at 60°C and weighed. The few plants that died prior to the end of the experiment were immediately removed and dried.

We examined all species in monoculture using a three-way ANOVA to evaluate significant effects of species, nutrients, and moisture on total biomass using SPSS 11.0 for Windows. Within species, we used a three-way ANOVA and Tukey's pairwise comparisons to evaluate significant effects of competition, nutrients, and moisture on total biomass and root:shoot ratio. To determine the importance of intra- and interspecific competition on total biomass, relative competitive yield (RCY) was calculated for each species combination as

$$\mathrm{RCY} = Y_{ij} \big/ Y_i$$

where Y_{ij} is the mean biomass of individuals of species i grown with species j and Y_i is the mean biomass of individuals of species i grown in monoculture (Harper 1977; Wetzel and van der Valk 1998). A RCY greater than one indicates that intraspecific competition had a greater effect on total biomass than interspecific competition, and a value less than one indicates that interspecific competition had a greater effect on total biomass than intraspecific competition. To test whether individual species combinations were significantly different than one, one-sample t tests were performed. For all analyses, pots were used as the replicate unit, and data were log-transformed to normalize the distribution of the residuals.

Results

Field experiment

Overall, differing degrees of aboveground vegetation removal affected the growth patterns in three of the four species (Table 1; Fig. 1). *Danthonia californica*, a native, did not produce more aboveground biomass in response to a reduction in neighbors, but plants with fewer neighbors had a greater basal area:height ratio, i.e., they were wider and shorter (Table 1; Fig. 1). Removing vegetation had no effect on aboveground biomass or the basal area:height ratio of *D. cespitosa*, the other native species (Table 1; Fig. 1). However, *D. cespitosa* grew marginally taller ($p = 0.055$) with more neighbors (data not shown). *Lolium multiflorum*, an exotic annual, was the only species to show an aboveground biomass response to vegetation removal, with the most aboveground biomass in the 100% aboveground competition reduction treatment (Table 1; Fig. 1). Similarly, the basal area:height ratio was greatest in the 100% competition reduction treatment (Fig. 1).

Table 1 Results of two-way ANOVA for aboveground biomass and basal area:height ratio of each species in the field experiment

	D. californica			*D. cespitosa*			*L. multiflorum*			*S. arundinaceus*		
	F	*df*	*p*	*F*	*df*	*p*	*F*	*df*	*p*	*F*	*df*	*p*
Aboveground biomass												
Competition	0.50	2	0.63	0.23	2	0.81	7.16	2	**0.005**	1.27	2	0.44
Block	15.3	3	**0.003**	3.46	1	0.20	2.46	1	0.13	4.52	1	0.17
Competition × Block	0.92	6	0.49	1.01	2	0.38	2.80	2	0.087	0.39	2	0.69
Basal area:height ratio												
Competition	21.8	2	**0.002**	2.19	2	0.14	14.2	2	**0.002**	18.8	2	**0.050**
Block	3.77	3	0.078	0.32	1	0.58	0.38	1	0.60	0.82	1	0.46
Competition × Block	0.98	6	0.45	2.09	2	0.15	1.08	2	0.36	0.16	2	0.85

P values <0.05 are in bold

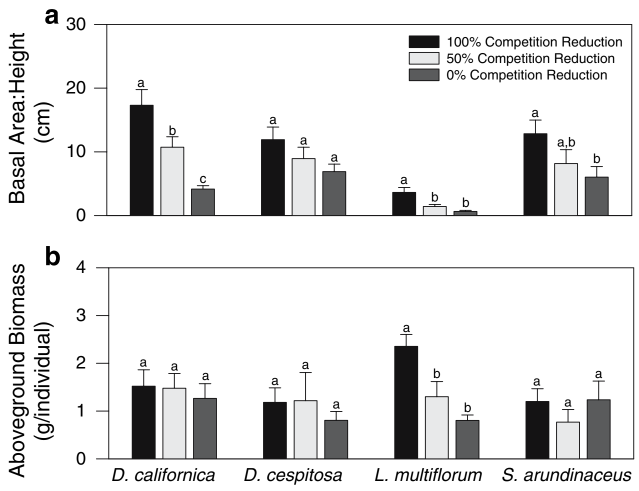

Fig. 1a–b Basal area:height (**a**) and aboveground biomass (**b**) of *Danthonia californica* ($n = 16$), *Deschampsia cespitosa* ($n = 8$), *Lolium multiflorum* ($n = 8$), and *Schedonorus arundinaceus* ($n = 8$) for 0, 50, and 100% competition reduction in the field. *Error bars* represent one standard error from the mean. *Lower case letter* differences indicate significant effects ($p < 0.05$) of competition within a species

Schedonorus arundinaceus, an exotic perennial, had a greater basal area:height ratio with 100% neighbor removal than in the 0% competition reduction treatment (Table 1; Fig. 1).

Greenhouse experiment

Plants in monoculture

To evaluate species growth responses to the nutrient and moisture treatments in the absence of the interspecific competition treatments, we analyzed results separately for the monoculture pots. Nutrient availability, moisture availability, species, and all of the interactions among these main effects significantly affected plant biomass ($p < 0.017$). Despite the significant interactions, clear differences in the amount of biomass produced by different species were evident (overall means = *D. californica* 0.0315 g ± 0.006, *D. cespitosa* 0.287 g ± 0.059, *S. arundinaceus* 2.629 g ± 0.325, *L. multiflorum* 3.688 g ± 0.059). In monoculture, native species produced less biomass than exotics ($p < 0.001$), and *L. multiflorum*, the only annual, produced significantly more biomass than the three perennial species ($p < 0.001$). Treatment effects on the species are discussed subsequently in terms of plants grown in combination with other species.

Interspecific competition (two-species polycultures)

The effect of nutrients on total biomass production in *D. californica* depended on moisture level (Table 2; Fig. 2). *D. californica* was only able to exploit the increase in nutrients in the high-moisture treatment. The competition treatment alone or in interaction with the nutrient or moisture treatments had no effect on *D. californica* (Table 2; Fig. 3). The ratio of roots to shoots depended upon moisture treatment; a greater proportion of the biomass was allocated to roots in the low-moisture treatment than in the high-moisture treatment (Table 2; Fig. 4).

Similarly, *D. cespitosa* responded positively to high nutrient concentrations only in the high-moisture treatment (Table 2; Fig. 2). *D. cespitosa* produced more biomass in monoculture than when grown with the exotic annual, *L. multiflorum* ($p = 0.027$), but the effect of the competition treatment never depended upon abiotic treatments (Table 2; Fig. 3). The root:shoot ratio of *D. cespitosa* decreased with higher nutrient availability (Table 2; Fig. 4).

Although *L. multiflorum* biomass was consistently greater in the high nutrient treatment, the effect of the competition treatment differed between low- and high-nutrient conditions (Table 2; Fig. 3). Under high-nutrient conditions,

Table 2 Results of three-way ANOVA for total biomass and root:shoot ratio of each species in the greenhouse experiment

	D. californica			*D. cespitosa*			*L. multiflorum*			*S. arundinaceus*		
	F	*df*	*p*	*F*	*df*	*p*	*F*	*df*	*p*	*F*	*df*	*p*
Total biomass												
Nutrients	2.34	1	0.13	12.2	1	**0.001**	191.2	1	**<0.001**	58.9	1	**<0.001**
Moisture	5.91	2	**0.004**	9.25	2	**<0.001**	0.53	2	0.59	3.29	2	**0.043**
Competitor Identity	0.46	3	0.71	3.28	3	**0.026**	5.77	3	**<0.001**	20.7	3	**<0.001**
Nutrients × Moisture	3.07	2	**0.053**	5.10	2	**0.009**	0.36	2	0.70	15.2	2	**<0.001**
Nutrients × Comp.	1.28	3	0.29	0.47	3	0.71	4.91	3	**0.004**	4.68	3	**0.005**
Moisture × Comp.	0.42	6	0.86	1.95	6	0.084	1.50	6	0.19	8.07	6	**<0.001**
Nutr. × Moist. × Comp.	0.52	6	0.74	0.33	6	0.92	0.59	6	0.74	0.91	6	0.49
Root:shoot ratio												
Nutrients	0.56	1	0.46	7.57	1	**0.008**	5.40	1	**0.023**	79.1	1	**<0.001**
Moisture	3.42	2	**0.038**	0.28	2	0.76	2.30	2	0.11	1.57	2	0.22
Competitor Identity	0.82	3	0.49	1.80	3	0.16	1.18	3	0.32	2.14	3	0.10
Nutrients × Moisture	0.87	2	0.42	1.44	2	0.25	0.71	2	0.50	1.75	2	0.18
Nutrients × Comp.	0.50	3	0.67	1.40	3	0.25	0.35	3	0.79	1.19	3	0.32
Moisture × Comp.	1.05	6	0.40	0.55	6	0.77	1.07	6	0.39	2.83	6	**0.016**
Nutr. × Moist. × Comp.	0.55	6	0.77	0.73	6	0.63	0.45	6	0.84	0.84	6	0.54

P values <0.05 are in bold

L. multiflorum was able to produce more biomass when grown with *S. arundinaceus* than in monoculture. However, under low-nutrient treatments, *L. multiflorum* produced more biomass when grown with *D. californica*. *L. multiflorum* allocated more biomass belowground in the low-nutrient treatment than in the high-nutrient treatment (Table 2; Fig. 4).

Total biomass of *S. arundinaceus* within moisture treatments depended on nutrient availability (Table 2; Fig. 2). Under high-nutrient conditions, *S. arundinaceus* had greater total biomass in the high-moisture treatment than in the medium-moisture treatment. There were no differences in total biomass among moisture levels in the low-nutrient treatment. Additionally, the response of *S. arundinaceus* to the competition treatment depended on nutrient availability (Table 2; Fig. 3). Total biomass did not differ between low- and high-nutrient levels when grown with *L. multiflorum*, suggesting that competition with *L. multiflorum* prevented *S. arundinaceus* from capitalizing on the increase in nutrient concentrations. Finally, the effect of the competition treatment on total biomass of *S. arundinaceus* also depended on moisture availability (Table 2). When grown with *D. cespitosa*, *S. arundinaceus* produced more biomass in the low-moisture treatment than in the medium-moisture treatment. When grown with *L. multiflorum*, the least amount of biomass was produced in the low-moisture treatment. A greater proportion of biomass was allocated to roots in the low-nutrient treatment (Table 2; Fig. 4). Additionally, the effect of the competition treatment on the root:shoot ratio depended upon moisture level; plants grown with *L. multiflorum* had a greater proportion of roots in the medium-moisture treatment than in the low-moisture treatment ($p = 0.043$).

Relative competitive yield

The RCY for each species was calculated across all nutrient and moisture treatments to determine the importance of intra- and interspecific competition on total biomass (Fig. 5). For the two exotic species, *L. multiflorum* and *S. arundinaceus*, the RCY was greater than one, suggesting intraspecific competition had a greater effect on total biomass than interspecific competition, with one exception: when *S. arundinaceus* was grown with *L. multiflorum*, the RCY was less than one ($p < 0.01$), suggesting that interspecific competition was more important than intraspecific competition. For the two native species, *D. californica* and *D. cespitosa*, the RCY was either less than or not significantly different than one, suggesting that intraspecific competition never exerted a greater influence on total biomass than interspecific competition. For *D. californica*, the RCY was less than one when grown with *D. cespitosa* ($p < 0.05$), and for *D. cespitosa*, the RCY was less than one when grown with the two exotics, *L. multiflorum* and *S. arundinaceus* ($p < 0.05$).

Discussion

The paired field and greenhouse studies strengthened our ability to understand how competition interacted with abiotic environmental variables to determine species dominance in a remnant prairie. In the field experiment, we were able to determine if competition, inferred from a removal of neighbors, is important within the natural environment, but as many environmental variables covary

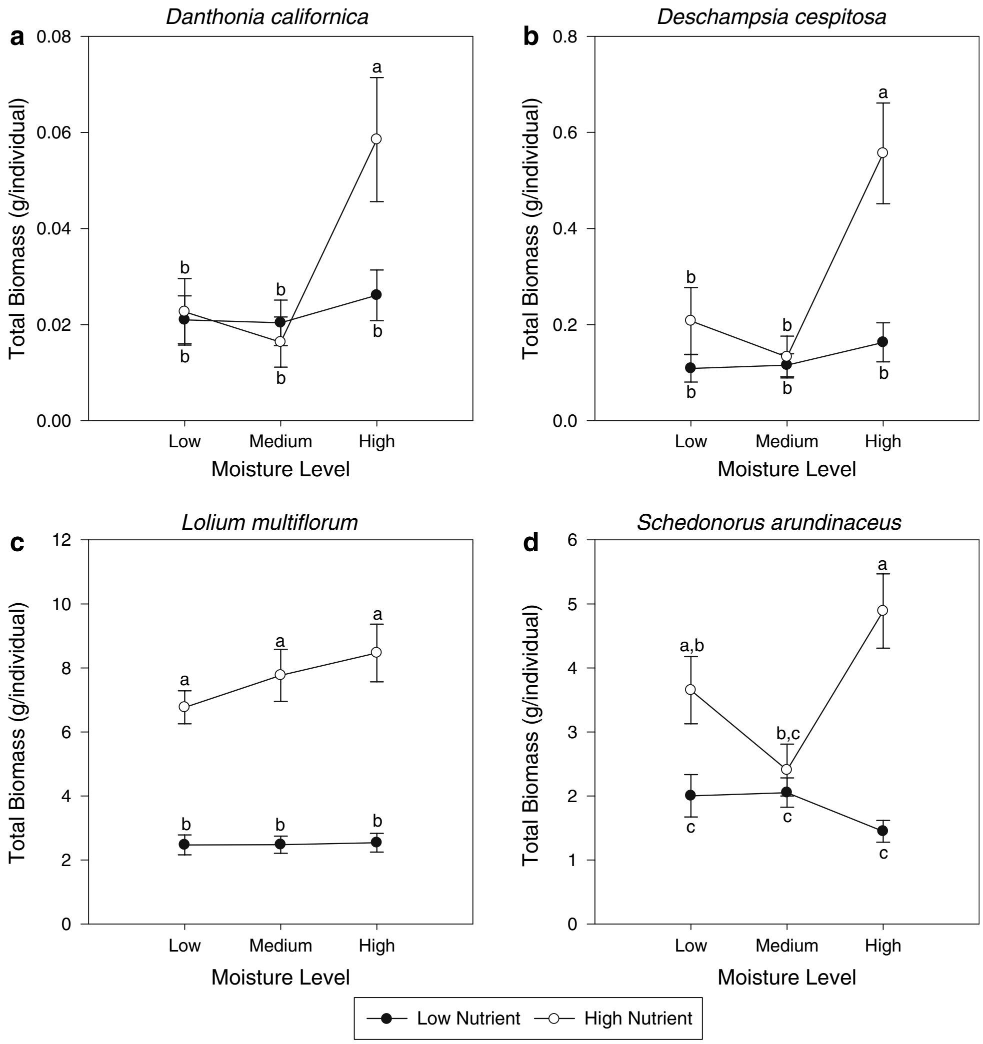

Fig. 2a–d Interaction between nutrients and moisture in the greenhouse experiment for total biomass of **a** *Danthonia californica*, **b** *Deschampsia cespitosa*, **c** *Lolium multiflorum*, and **d** *Schedonorus arundinaceus* ($n = 16$) across all species combinations. *Error bars* represent one standard error from the mean. *Different lower case letters* indicate significant ($p < 0.05$) treatment effects

and are not easily isolated in the field, we moved to the greenhouse to tease apart how nutrients, moisture, and competition interacted to determine species dominance. Previous research conducted in 2003 and 2004 (L. Pfeifer-Meister et al., manuscript in preparation) showed that the relative distribution of native and exotic species was correlated with moisture and nutrient availability, with a higher proportion of native species biomass occurring in nutrient-poor, wet sites. In the mesic areas, exotic grasses appeared to form dense monocultures (Simpson's diversity vs. exotic grass biomass; $r = -0.69$, $p = 0.003$), which we hypothesized was due to the competitive exclusion of native species from these environments. The exclusion of native species could also be explained by their limited seed availability, rather than by their low competitive ability (Seabloom et al. 2003a, 2003b). However, neighboring stands of each species provided ample seed supply across the prairie, so seed limitation was unlikely within our study area.

In our field experiment, we verified the four grass species were competing within the natural environment. The amount of aboveground competition influenced plant morphology; all four species grew to cover at least a marginally larger area and/or shorter height when surrounding vegetation was removed. These changes in morphology will likely translate into increased biomass and seed count during successive seasons due to increased light capture ability (Schmitt and Dudley 1996). Similarly, Wilson and Shay (1990) found that basal circumference increased in perennial grasses when neighbors were removed in a Canadian mixed-grass prairie. *L. multiflorum*, the only non-perennial, was able to capitalize on the reduction in competition to produce more aboveground biomass, which was highly correlated ($r = 0.92$) with seed production.

The greenhouse experiment supported our main hypothesis that competitive hierarchies change with abiotic conditions, but only for the two exotic grasses. The

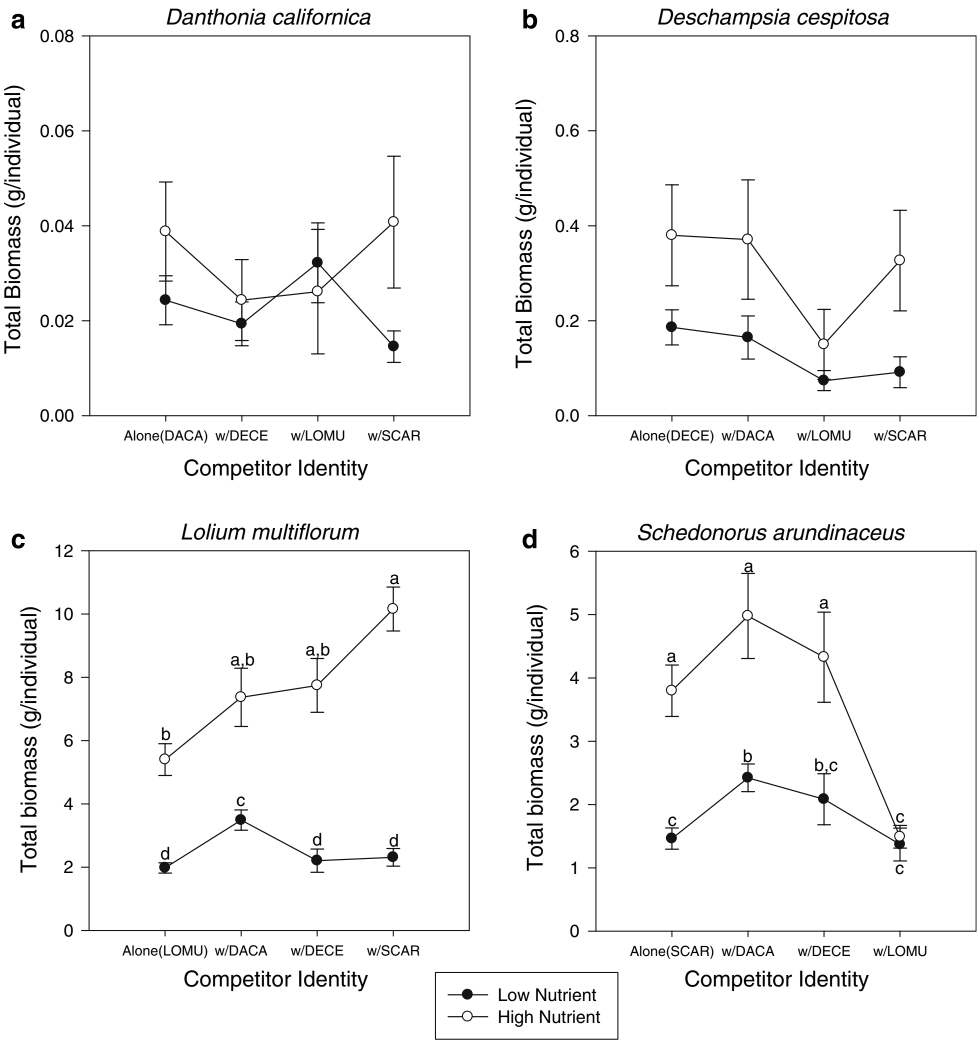

Fig. 3a–d Total biomass per individual of **a** *Danthonia californica*, **b** *Deschampsia cespitosa*, **c** *Lolium multiflorum*, and **d** *Schedonorus arundinaceus* among competition levels (monoculture: alone; interspecific competition: *w/SCAR* with *S. arundinaceus*, *w/LOMU L. multiflorum*, *w/DACA* with *D. californica*, *w/DECE* with *D. cespitosa*) for low- and high-nutrient concentrations in the greenhouse ($n = 12$). *Error bars* represent one standard error from the mean, and *lower case letter* differences indicate significant effects ($p < 0.05$)

competitive success of *L. multiflorum* and *S. arundinaceus* depended upon nutrient availability (Fig. 3), and the competitive success of *S. arundinaceus* further depended upon moisture. However, the details of these interactions did not clearly support our more specific hypothesis that aggressive exotic species have a greater competitive ability at high-nutrient, moderate-moisture conditions. Under low-nutrient conditions, *L. multiflorum* produced the most biomass when in competition with *D. californica*, whereas in high-nutrient treatments, *L. multiflorum* produced the most biomass when in competition with *S. arundinaceus*. *L. multiflorum* is the stronger competitor of the two exotics, as it was able to prevent *S. arundinaceus* from capitalizing on high nutrient availability (Fig. 3). This was also supported in the relative competitive yield calculations, where intraspecific competition always had a greater effect on *L. multiflorum* than interspecific competition, and the only competitive interaction for *S. arundinaceus* that had a greater influence on total biomass than intraspecific competition was with *L. multiflorum. L. multiflorum* is an annual, and this may reflect annual grasses being generally more competitive than perennial grasses under high-nutrient conditions. For example, Lowe et al. (2003) showed that as nitrogen availability increased, the annual exotic grass *Bromus tectorum* dominated the native perennial grass *Bouteloua gracilis*, and intraspecific competition was more significant than interspecific competition for the exotic grass, while the reverse was true for the native grass.

Abiotic factors never affected the competitive outcome for the two native species, *D. cespitosa* and *D. californica*, in the greenhouse. The native *D. cespitosa* was least competitive when in combination with *L. multiflorum*, but this did not depend on moisture or nutrient conditions. In general, the two native species attained a much smaller size than the two invasive species, and their biomass production and allocation appeared to be primarily controlled by abiotic factors and not competition (Figs. 2, 4). Although this result is consistent with findings in other West Coast prairies (Bakker and Wilson 2001; Corbin and D'Antonio 2004), some studies have observed an interaction between

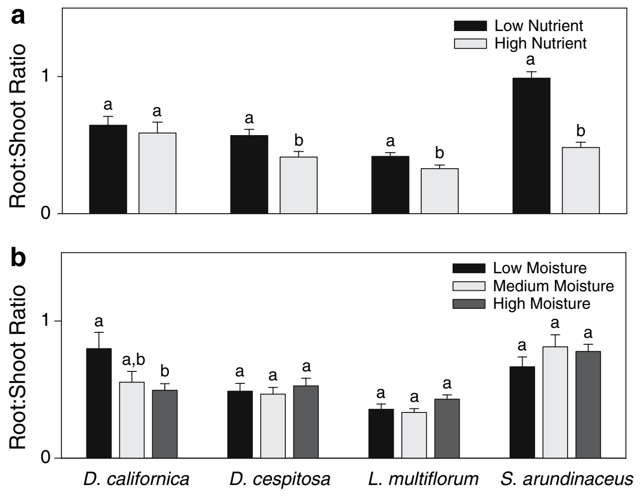

Fig. 4a–b Ratio of roots to shoots in the greenhouse of *Danthonia californica*, *Deschampsia cespitosa*, *Lolium multiflorum*, and *Schedonorus arundinaceus* among nutrient concentrations (**a**, $n = 48$) and moisture levels (**b**, $n = 32$). *Error bars* represent one standard error from the mean, and *lower case letter* differences indicate significant effects ($p < 0.05$) within species

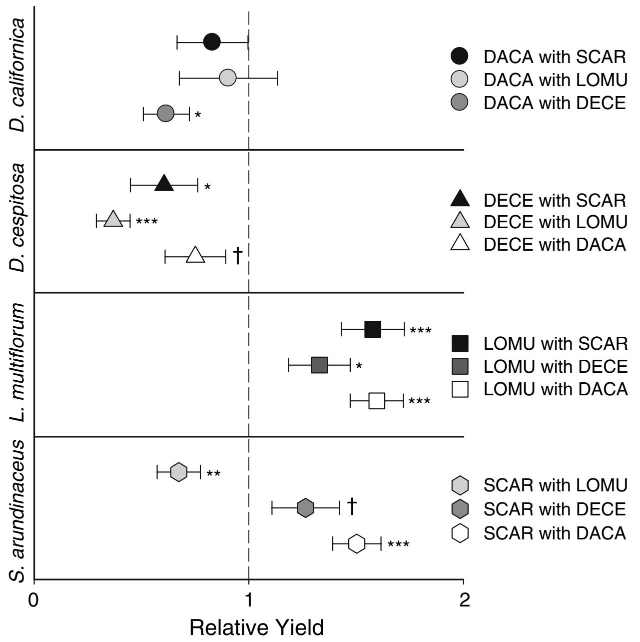

Fig. 5 Total biomass relative competitive yield (± standard error) for *Danthonia californica* (*DACA*), *Deschampsia cespitosa* (*DECE*), *Lolium multiflorum* (*LOMU*), and *Schedonorus arundinaceus* (*SCAR*) in the greenhouse ($n = 24$). Values less than one indicate that interspecific competition is greater than intraspecific competition, and values greater than one indicate that intraspecific competition is greater than interspecific competition. Each species combination was tested if significantly different than one (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, † = $p < 0.10$)

abiotic factors and competition for native species. For example, in a California montane meadow, the competitive ability of *D. cespitosa* decreased at very low soil moisture (Kluse and Allen Diaz 2005). In a California grassland, the native perennial, *Sporobolus airoides*, had lower survival at higher ammonium concentrations when in competition with the exotic annual, *Bromus diandrus* (Hoopes and Hall 2002). However, in this latter study, differences in timing of establishment could explain this effect. Rather than planting germinated seedlings into their competition plots, seeds were scattered and allowed to establish naturally. In our study site, the annual exotic grasses, including *L. multiflorum*, germinate much earlier than the perennial natives (personal observation). As we did not consider timing of germination in our experiment, we are not able to rule out the possibility that natives are excluded from the mesic habitats due to differences in establishment dates.

Three of the grasses had the greatest growth response to high nutrients at the highest moisture level (Fig. 2). The exception was *L. multiflorum*, which consistently produced more biomass under high nutrient conditions regardless of moisture availability. In addition, *D. cespitosa*, *L. multiflorum*, and *S. arundinaceus* allocated more resources belowground in the low-nutrient treatment, and *D. californica* had a higher root:shoot ratio in the low-moisture treatment than in the high-moisture treatment (Fig. 4). The competitiveness of *S. arundinaceus* depended on moisture, but in a complicated manner that did not support our hypothesis.

The field experiment supported the importance of competition in situ, and the greenhouse experiment supported our main hypothesis that competitive hierarchies change depending on abiotic conditions, but only for the two exotic species. However, our more specific hypothesis, that the aggressive exotic species, *S. arundinaceus* and *L. multiflorum*, have a greater competitive ability at high-nutrient, moderate-moisture conditions, was not consistent with the results from the greenhouse experiment. Furthermore, we found no support for the idea that native species were preferentially excluded from nutrient-rich, moderately wet environments, but we cannot rule out timing of germination as an important factor in contributing to the exclusion of native species in the field. The large average size of *L. multiflorum* when grown in monoculture, its large absolute and relative response to nutrient additions irrespective of moisture conditions, and its greater overall competitiveness in the greenhouse pairs support a conclusion that this invasive species is a very potent competitor with both native and exotic species. However, the competitive ability of perennial species may increase over multiple growing seasons. The factors contributing to plant community structure are complex, but our experiment shows that even within a single growing season, competition, nutrients, and moisture influence plant success and determine interactions between native and exotic species.

Acknowledgments We thank C. Cherrier, J. Davis, D. Fournier, L. Gayton, K. Sonnenblick, J. Talbot, J. Thompson, L. Turnbull, and A. Winterle for field and lab assistance, B. Johnson for his preliminary work in establishing the four blocks, and D. Todd, J. Stewart, K. Blaisdell, and two anonymous reviewers for valuable comments on earlier drafts of this manuscript. We also thank Friends of Buford Park and Lane County Parks for use of our field site, Mt. Pisgah. This research was partially supported by the U.S. Environmental Protection Agency through the Lane Council of Governments and the West Eugene Wetlands Partnership, the U.S. Environmental Protection Agency's STAR program, and the Robert D. Clark's Honors College, University of Oregon. Although the research described in the article has been funded in part by the U.S. Environmental Protection Agency's STAR program to L. P-M., it has not been subjected to any EPA review and therefore does not necessarily reflect the views of the Agency, and no official endorsement should be inferred.

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