

OAK CANOPY EFFECTS ON THE DISTRIBUTION PATTERNS OF TWO ANNUAL GRASSES: THE ROLE OF COMPETITION AND SOIL NUTRIENTS¹

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Within the oak woodlands of California there is often a distinct shift in the botanical composition between the open grassland and the herbaceous understory beneath oak canopy. Botanical sampling at two woodland sites indicated that the annual grass *Bromus diandrus* was dominant under deciduous blue oak canopy, while a congener, *Bromus hordeaceus*, was dominant in open grassland. We examined the relative importance of congeneric competition and edaphic factors in creating these differences in species distribution in two separate field experiments that manipulated both congeneric and intraspecific competition, as well as soil type. We used the demographic measure of relative reproductive rate as an index of population growth. In general, demographic performance correctly predicted the distribution of the two annual grasses in the field. Our results indicate that reduced abundance of *B. hordeaceus* under canopy reflects the negative effects of competition with *B. diandrus*. In contrast, *B. diandrus* is little affected by competition from *B. hordeaceus*. The reduced abundance of *B. diandrus* in open grassland may result, in part, from its inability to adapt as well as *B. hordeaceus* to lower nutrient availability in soils of the open grassland.

Key words: annual grasses; *Bromus*; California; oak canopy; plant competition; Poaceae; *Quercus*; soil nutrients; species distribution.

Within woodland and savanna communities worldwide, one of the most obvious local gradients in species distribution occurs between the understory of trees and adjacent open grassland (Curtis, 1959; Ebersohn and Lucas, 1965; Parker, 1977; Schott and Pieper, 1985; Scholes and Walker, 1993; Vila and Sardans, 1999; Weltzin and McPherson, 1999). In California oak woodlands and savannas, species compositional shifts between open grassland and understory vegetation are often well developed and have been found within both deciduous and evergreen oak communities (Holland, 1973; Parker and Muller, 1982; McClaran and Bartolome, 1989; Callaway and Davis, 1998). Studies on mechanisms causing differences in species composition under oak canopy usually have emphasized differential adaptation to canopy-caused gradients in soil nutrients and light (Holland, 1973; Mahall, Parker, and Fonteyn, 1981; Maranon and Bartolome, 1993; Dahlgren, Singer, and Huang, 1997; Davis, Wrage, and Reich, 1998; Davis et al., 1999). Although Maranon and Bartolome (1993) suggest that herbaceous competition under dense evergreen oak stands is weak, the importance of competition in affecting changes in composition under deciduous oaks is unknown. In addition, despite the long-standing interest in the competitive interactions between congeners (Tansley, 1917; Harper et al., 1961;

Marshall and Jain, 1967; Werner and Platt, 1976), there are surprisingly few studies that have used experimental manipulations in the field to examine how competition between congeners along an environmental gradient may contribute to observed shifts in species composition and dominance (but see Grace and Wetzal, 1981).

Throughout much of the range of blue oak (*Quercus douglasii* Hook & Arn.) woodlands in California, the annual grass *Bromus diandrus* Roth typically dominates under the canopy of this deciduous oak, while a congener, *B. hordeaceus* L., is usually dominant in the adjacent open grassland (Holland, 1973; McClaran and Bartolome, 1989). In order to use this woodland system to examine the effect of competition between congeners on plant species distribution, we conducted a field experiment that examined how the competitive balance between *B. diandrus* and *B. hordeaceus* changed between open grassland and blue oak understory. We measured the performance of each species using a demographic index (i.e., relative reproductive rate) that (1) facilitated comparisons of performance between species and (2) allowed us to examine whether the population performance of a species correctly predicted its distribution and abundance. Because it has been suggested that increases in soil nutrients beneath blue oak canopy may be important in causing this shift in distribution (Holland, 1973), we also manipulated soil type in order to examine edaphic effects independently of competition and other environmental factors such as shading. Finally, we repeated the entire experiment at another site in the following year. Because we used a different site in the second year, we could not partition site and year effects; however, this second year of the experiment did allow us to examine the robustness of our results across different growth environments.

MATERIALS AND METHODS

The climate of both field sites used in this study is Mediterranean with cool, wet winters and hot, dry summers. The Hopland Research and Extension

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Center (Mendocino County, California, USA) is located within the inner coast range of north-central California (39° N, 123°5' W) at an elevation of 370 m and receives an average annual precipitation total of 92.6 cm (Hopland station records, 44-yr record). The Sierra Foothill and Extension Center (Yuba County, California) is located in the Sierra Nevada foothills (39°16' N, 121°17' W) at an elevation of 400 m and receives an average annual precipitation total of 72.4 cm (Sierra station records, 32-yr record). At both sites, > 90% of the precipitation occurs between October and May with only trace amounts during the summer months. Both sites are characterized by an oak overstory dominated by deciduous blue oak (*Quercus douglasii*). The understory and adjacent open grasslands are dominated by introduced Mediterranean annual species, especially grasses, that have become widely naturalized throughout California grasslands (Heady, 1977). The modal texture of the soils at the Hopland site is silty loam (ultic haploxeroll), while the soil texture at the Sierra site is rocky loam (mollic haploxeralf). The Hopland site is grazed by sheep, while the Sierra site has been grazed primarily by cattle.

At both field sites, we used a split-plot design with habitat type (grassland or oak canopy) as the main plot factor and species, soil type, and density of each *Bromus* species as factorial subplot factors. At each site we established five rectangular (30 × 10 m) replicate blocks under different blue oak trees. These blocks were fenced to prevent livestock grazing and were oriented at random with respect to compass direction. Blocks were located near each tree so that approximately one-third of the block (10 × 10 m) was under canopy, one-third in open grassland, and one-third of the block was located in a transition zone between the two habitats. The transition area of the block was not used for planting. We planted the blocks at Hopland on 9–13 September 1987 before the onset of the rainy season. Similarly in the following year, we planted before fall rains at Sierra on 5–8 September 1988. Hereafter, for convenience, we will refer to the separate experiments by their field sites, but it should be noted that differences between the field experiments represents the combined effects of both site and year. We examined the influence of soil nutrients on compositional shifts between habitats by using a reciprocal transplant approach. Thirty-two 20 cm diameter holes were augured within each replicate block to a depth of 30 cm, 16 in the oak canopy main plot and 16 in the grassland main plot. Although some roots may penetrate more deeply than 30 cm, studies on root distribution of these annual grass species indicate that the majority of roots occur in this upper layer of soil (Gordon and Rice, 1992, 1993; Holmes and Rice, 1996). The 16 holes within each main plot were arranged in a four by four array with a 50-cm spacing. We collected and bulked the soil from the 16 holes within each habitat type. From each bulk collection, soil was either refilled into the holes within the original habitat or transplanted to holes within the other habitat. Within each main plot, these refilled holes served as the planting locations for the various subplot treatment combinations. Removal and refilling of soil for all the planting subplots provided the necessary experimental controls for the disturbance caused by transplanting soils. When replacing the soil, we compacted the soil as much as possible, however, measurements taken from a set of test holes indicated that the bulk density of transplanted soil was less than that of undisturbed soil. Because of this reduction in bulk density, we were unable to examine the influence of bulk density variation as a factor causing compositional shifts across habitats. Although effects of bulk density variation on species shifts could not be examined experimentally, from each of the five blocks we removed cores of undisturbed soil (20 cm depth) in open grassland and under oak canopy to examine bulk density variation. To test for soil nutrient differences along this gradient, subsamples of the bulk density cores were submitted to the University of California Division of Agriculture and Natural Resources Analytical Laboratory for analysis of total Kjeldahl nitrogen, phosphorus, and exchangeable potassium, calcium, and magnesium. Differences between field sites and habitats in soil characteristics were analyzed as a randomized complete block design using the General Linear Model procedure in the SAS statistical package (Freund, Littell, and Spector, 1986).

At each field site, differences in the light and temperature environment of each habitat were measured when the oak trees were leafless (February) and when the trees had developed full leaf canopy (April). Using a sun-fleck ceptometer (Decagon Instruments, Pullman, Washington, USA), photosynthetic photon flux density (PPFD) was measured at five points within each

canopy subplot and expressed as a percentage of the average PPFD measured for the adjacent grassland subplot. Air temperatures at a height of 10 cm were measured with a thermocouple thermometer (Decagon Instruments) at five points within both canopy and open grassland subplots; any canopy effects were expressed as a difference between canopy and open grassland temperatures. Both PPFD and air temperatures were measured between 0900 and 1000, 1200 and 1300, and 1600 and 1700. A repeated-measures analysis was used to detect effects of season, time of day, and site on light and temperature differences between habitats; canopy PPFD data, expressed as a percentage of open grassland PPFD, were angular (arcsine) transformed before analysis.

In order to document species composition shifts between open grassland and oak understory, we measured species cover using a stratified random sampling design. A point sampling frame developed for sampling annual vegetation (Heady and Rader, 1958) was located at 20 randomly selected locations within each main plot, resulting in a total of 200 points per main plot. To facilitate identification at both field sites, we made these measurements when most annual species were flowering (Hopland—10 May 1988; Sierra—5 May 1989). Changes in composition between open grassland and understory habitats were analyzed as a randomized complete block design with habitat type and field site as factors. As noted above, because a different field site was used in each year, the joint effects of site and year cannot be separated statistically. In addition to analyzing the absolute cover data of both *Bromus* species, we also analyzed total cover as well as cover data for the other most common grass (*Avena barbata* Link) and forb species (*Erodium cicutarium* L'Her.). Percent cover data were angular transformed before analysis by the GLM procedure in SAS.

To test the potential importance of competition among congeners in causing shifts in dominance between the two *Bromus* species, demographic responses to changes in the density of conspecifics and congeners were monitored for both species. Planting densities for both species were 45, 90, 135, and 270 seeds/dm². These planting densities represent a range that is typical for these grass species in the California annual grassland (Heady, 1958). Seeds of *Bromus diandrus* and *B. hordeaceus* used in plantings at Hopland were collected from six different populations at this site on 3–5 June 1987, while seeds for the experiment at Sierra were collected from eight populations at Sierra on 24–26 May 1988. We estimated population growth rate (relative reproductive rate) by dividing seed output per plot by seed input (i.e., planting density per plot). To reduce edge effects, we harvested plants only from the central 15 cm diameter area of each plot, resulting in a 2.5-cm buffer around the edge of the plot.

Data were analyzed as a split-plot design using the GLM procedure of the SAS statistical package (Freund, Littell, and Spector, 1986). Estimates of seed output required for the calculation of relative reproductive rate (RRR) were obtained from regressions relating seed mass to seed number. In order to properly compare relative reproductive rates across treatment combinations, it was necessary to confirm that reproductive parameters other than seed number (i.e., individual seed mass) were not affected by the treatments (except species identity). In order to test this assumption, we examined treatment effects on individual seed mass from a random subsample of seeds from the experimental subplots. To meet parametric assumptions of the linear model, individual seed masses and relative reproductive rates were ln-transformed before analysis. For each site (Sierra 1988–1989 and Hopland 1987–1988), the potential interactive effects of the various factors were examined by testing the significance of all interaction components, beginning with the highest order (i.e., five-way) interaction. Interactions that were significant ($P < 0.05$) were then further studied by inspection of plots of the appropriate interacting factors.

RESULTS

Botanical composition and physical environment of grassland and oak canopy plots—Analysis of the mean cover data (Tables 1, 2) indicates that *B. diandrus* is consistently more abundant under canopy and a minor component in open grassland at both sites. On the other hand, although *B. hordeaceus* is definitely more abundant in the open grassland at

TABLE 1. Analysis of variance of effects of habitat type (open grassland vs. understory) and site (Hopland vs. Sierra) on total cover and absolute cover of the four most common annual species.

Source	df	Type III SS	MS	F	P
A) <i>Bromus diandrus</i>					
Site	1	0.01916	0.01916		
Habitat	1	0.56540	0.56540	4.3	<0.05
Block	4	0.01786	0.00446	128.2	<0.0001
Site × Habitat	1	0.00992	0.00992	1.0	>0.20
Error	12	0.05292	0.00441	2.2	>0.10
B) <i>Bromus hordeaceus</i>					
Site	1	0.02231	0.02231	5.8	
Habitat	1	0.20397	0.20397	53.4	<0.05
Block	4	0.02080	0.00520	1.4	<0.0001
Site × Habitat	1	0.07309	0.07309	19.2	>0.20
Error	12	0.04580	0.00382		<0.001
C) <i>Avena barbata</i>					
Site	1	0.01032	0.01032	1.2	>0.20
Habitat	1	0.00179	0.00179	0.2	>0.50
Block	4	0.00397	0.00099	0.1	
Site × Habitat	1	0.00022	0.00022	0.02	>0.50
Error	12	0.10788	0.00899		>0.50
D) <i>Erodium cicutarium</i>					
Site	1	0.02300	0.02300	27.0	<0.001
Habitat	1	0.51202	0.51202	601.5	
Block	4	0.00665	0.00166	2.0	<0.0001
Site × Habitat	1	0.02300	0.02300	27.0	>0.10
Error	12	0.01022	0.00085		<0.001
E) Total cover					
Site	1	0.00002	0.00002	0.00	>0.50
Habitat	1	0.01513	0.01513	1.62	
Block	4	0.05846	0.01462	1.57	>0.20
Site × Habitat	1	0.01974	0.01974	2.12	>0.20
Error	12	0.11176	0.00931		>0.10

the Hopland site in 1988, this difference (although significant) is not as distinct at the Sierra site in the following year. The cover of *Avena barbata* did not vary much between habitats while *Erodium cicutarium* was absent under canopy.

A comparison of soil nutrient levels between open grassland and oak canopy plots indicated that total nitrogen, phosphorus, potassium, and calcium levels were significantly higher under canopy ($P < 0.05$), while no difference ($P > 0.10$) was detected for magnesium (Table 3). These patterns were consistent for both Hopland and Sierra field sites.

Repeated-measures ANOVA of data on differences in PPFD between canopy and open grassland indicated a significant interaction between season of measurement and time of day that a light measurement was taken ($F_{\text{Time} \times \text{Month}} = 19.8$; $P < 0.0001$). This interaction reflected the fact that because trees were fully leafed-out during the April measurements, the canopy light levels were lowest relative to ambient at mid-day when the sun was near its highest azimuth for the day (Fig.

TABLE 2. Absolute percent cover values under canopy and in open grassland at both field sites for the four most common herbaceous species (mean \pm 1 SD). Within each field site, mean cover values with the same superscript are not significantly different ($P > 0.05$). Although analysis was performed on angular transformed data, untransformed values are presented in the table.

Species	Hopland Field Site		Sierra Field Site	
	Open grassland	Under canopy	Open grassland	Under canopy
<i>Bromus diandrus</i>	1.5 \pm 1.2 ^a	22.2 \pm 6.7 ^b	0.9 \pm 0.7 ^a	14.0 \pm 4.3 ^b
<i>Bromus hordeaceus</i>	15.8 \pm 4.3 ^a	1.0 \pm 1.0 ^b	12.2 \pm 4.5 ^a	7.4 \pm 3.4 ^b
<i>Avena barbata</i>	3.4 \pm 3.0 ^a	2.8 \pm 1.9 ^a	4.8 \pm 3.1 ^a	3.8 \pm 2.4 ^a
<i>Erodium cicutarium</i>	14.4 \pm 2.9 ^a	0.0 \pm 0.0 ^b	6.4 \pm 2.5 ^a	0.0 \pm 0.0 ^b
Total plant cover	54.2 \pm 8.2 ^a	47.6 \pm 7.0 ^a	52.8 \pm 14.7 ^a	53.6 \pm 8.9 ^a

TABLE 3. Total nitrogen and phosphorus and exchangeable potassium, calcium, and magnesium (mg/g soil) in soils (0-20 cm deep) in open grassland and under oak canopy at both field sites (mean \pm 2 SE). Within each field site, average nutrient values with the same superscript are not significantly different ($P > 0.05$).

Nutrient (mg/g soil)	Hopland field site		Sierra field site	
	Open grassland	Under canopy	Open grassland	Under canopy
Nitrogen	2.3 \pm 0.8 ^a	7.4 \pm 1.7 ^b	2.9 \pm 0.7 ^a	5.0 \pm 1.2 ^b
Phosphorus	0.4 \pm 0.1 ^a	0.7 \pm 0.1 ^b	0.3 \pm 0.1 ^a	0.6 \pm 0.2 ^b
Potassium	1.8 \pm 0.3 ^a	2.4 \pm 0.4 ^b	1.6 \pm 0.2 ^a	2.1 \pm 0.3 ^b
Calcium	2.0 \pm 0.1 ^a	2.7 \pm 0.3 ^b	1.4 \pm 0.1 ^a	2.2 \pm 0.2 ^b
Magnesium	0.9 \pm 0.1 ^a	1.1 \pm 0.2 ^a	1.0 \pm 0.1 ^a	1.3 \pm 0.2 ^a

1). In contrast, there was no significant diel trend in February when the trees were leafless. Repeated-measures analysis of temperature differences indicate that the fully developed canopies present in April reduce understory temperatures significantly from mid-day to late afternoon (Fig. 2); however, there is no diel trend in February when the trees are leafless ($F_{\text{Time} \times \text{Month}} = 53.4$; $P < 0.0001$).

Although the cumulative total rainfall for each field site was very similar (Fig. 3), 1987–1988 represented a lower than average rainfall year for the Hopland site. Beginning in March, rainfall was below normal throughout the spring growing season. At the Sierra site, lower than average rainfall during January and February of 1988–1989 was followed by average rainfall during the spring growing season.

Relative reproductive rate (RRR)—Analysis of the effects of the treatments on individual seed mass indicated that, as expected, individual seed mass varied strongly between species (mean \pm 1 SE; *B. hordeaceus* = 1.65 \pm 0.013 mg; *B. diandrus* = 6.92 \pm 0.015 mg). However, no other treatment factor had a significant effect on individual seed mass despite good statistical power to detect differences. The high power of the analysis is indicated by the fact that for all treatment combinations, the coefficient of variation for the mean response was always less than 5%. As a result, any effects that the treatments might have on individual seed mass would have to be very small to not be detected by the analysis. These results indicate that the use of seed number alone as a response variable to estimate reproductive fitness is justified and is not confounded by significant changes in individual seed mass.

The overall ANOVA model for relative reproductive rate (RRR) was highly significant at both sites ($P < 0.001$) and explained 77.2% (Hopland) and 81.2% (Sierra) of the variance in relative reproductive rate (Table 4).

Hopland Site (1987–1988)—Habitat by species interactions

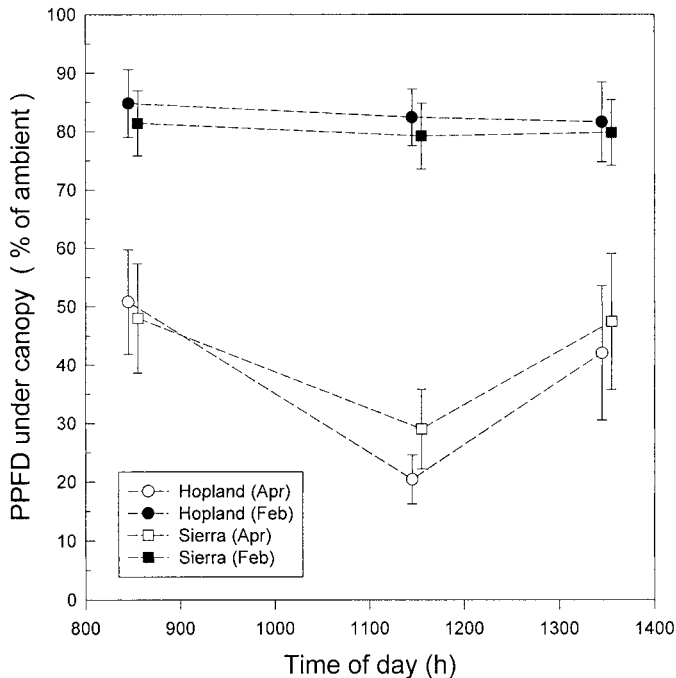


Fig. 1. Seasonal variation (February vs. April) in diel patterns of photosynthetic photon flux density (PPFD) under canopy at both the Hopland and Sierra field sites. Average PPFD values (± 1 SD) under canopy are expressed as % of ambient PPFD.

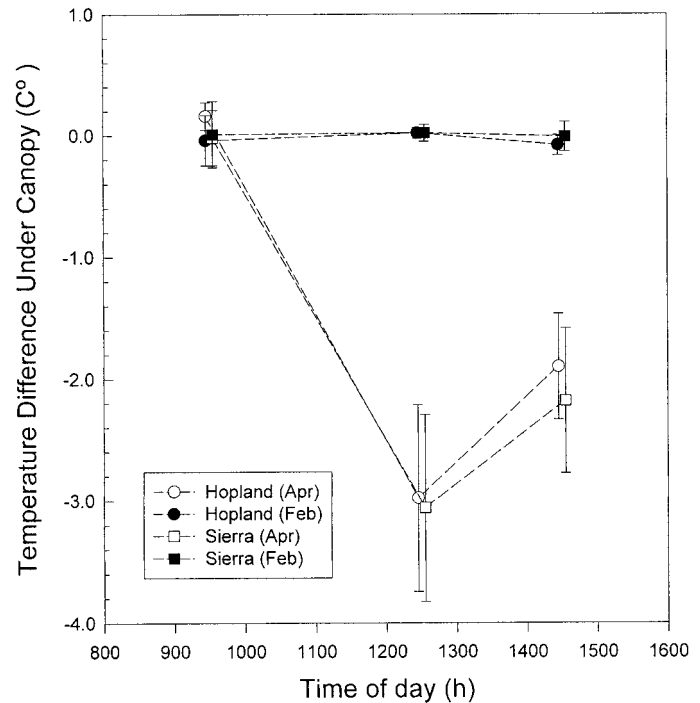


Fig. 2. Seasonal variation (February vs. April) in diel patterns of average air temperature differentials (± 1 SD) between canopy and open grassland habitats at both field sites.

in relative reproductive rate were quite pronounced (Table 4A), such that the population growth for a *Bromus* species depended strongly on whether it was under canopy or in open grassland (Fig. 4). Relative reproductive rates were positive and high for *B. hordeaceus* populations in grassland plots, while populations of *B. diandrus* exhibited negative growth rates in this habitat. Conversely, under canopy the population growth rates of *B. diandrus* populations were positive, while growth rates in *B. hordeaceus* populations were near zero.

Although relative reproductive rates for both species were greater overall in oak soil than in grassland soil at the Hopland site ($RRR_{oak} = 3.68$ vs. $RRR_{grass} = 2.08$; $P < 0.001$), there was a significant soil by species interaction (Table 4A, Fig. 5A). Population growth of *B. diandrus* in grassland soil was 65% lower than in oak soil ($RRR_{oak} = 4.55$ vs. $RRR_{grass} = 1.58$), while the decrease in *B. hordeaceus* population growth was only 8% ($RRR_{oak} = 2.80$ vs. $RRR_{grass} = 2.57$).

A significant species by *B. diandrus* density interaction (Table 4A, Fig. 6A) indicates that, as the density of *B. diandrus* increased, the RRR of *B. hordeaceus* was reduced to a greater extent than that of *B. diandrus*. In contrast, changes in the density of *B. hordeaceus* did not have a significant effect on the RRR of either species (Table 4A). Taken together, these results indicate that *B. diandrus* is a stronger interspecific competitor than *B. hordeaceus*.

Sierra Site (1988–1989)—As found for the Hopland site, relative reproductive rates averaged across both species at the Sierra site were greater in oak soil than in grassland soil ($RRR_{oak} = 10.99$ vs. $RRR_{grass} = 5.20$; $P < 0.05$) and soil effects significantly interacted with species (Table 4B and Fig. 5B; $P < 0.01$). Population growth of *B. diandrus* in grassland soil was 71% lower than in oak soil ($RRR_{oak} = 14.27$ vs. $RRR_{grass} = 4.16$), while the decrease in the growth of *B. hordeaceus* populations planted in grassland soil was only 19% ($RRR_{oak} = 7.71$ vs. $RRR_{grass} = 6.24$).

A strong two-way interaction between species and *B. diandrus* density indicated that, similar to the Hopland site, *B. diandrus* appeared to be a stronger interspecific competitor than *B. hordeaceus* (Table 4B, Fig. 6B). In addition, a significant three-way interaction at the Sierra site (Table 4B; $P < 0.05$) among habitat type, species, and density of *B. diandrus*

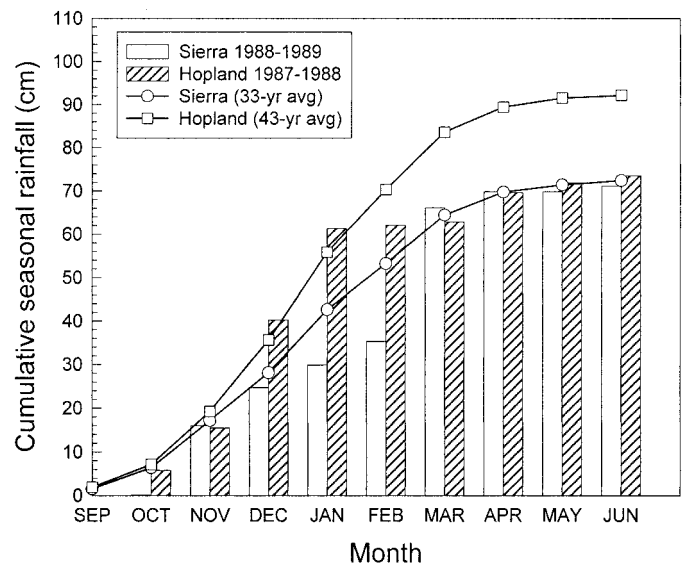


Fig. 3. Cumulative seasonal rainfall at Hopland (1987–1988), Sierra (1988–1989), and the long-term average at both field sites.

TABLE 4. Analysis of variance results for relative reproductive rate (RRR) data (ln transformed) at both the Hopland and Sierra field sites. Relative reproductive rate was estimated by dividing seed output per plot by seed input (i.e., planting density per plot). Results for treatment main effects are presented even if not statistically significant (i.e., $P > 0.05$). Habitat main effects were tested over the block \times habitat MS because of the split plot design. Because of the large number of potential treatment interactions, only interactions that were significant ($P < 0.05$) are presented in the table.

Source of variation	df	MS	F	P
A) Relative reproductive rate (ln-transformed) at Hopland				
Total model	31	4.571	13.03	<0.001
Block	4	2.375	6.77	<0.01
Habitat	1	0.149	0.37	>0.20
Soil	1	4.761	13.57	<0.001
Species	1	0.699	1.99	>0.10
<i>B. diandrus</i> density	1	11.840	33.75	<0.0001
<i>B. hordeaceus</i> density	1	1.063	3.03	>0.05
Habitat \times Species	1	14.160	40.37	<0.0001
Soil \times Species	1	2.133	6.08	<0.01
Species \times <i>B. diandrus</i> density	1	6.386	18.20	<0.001
Error	119	0.3508		
B) Relative reproductive rate (ln-transformed) at Sierra				
Total model	31	4.815	13.24	<0.001
Block	4	2.681	7.37	<0.01
Habitat	1	8.303	16.05	<0.001
Soil	1	1.932	5.32	<0.05
Species	1	2.564	7.05	<0.05
<i>B. diandrus</i> density	1	11.840	32.57	<0.01
<i>B. hordeaceus</i> density	1	1.118	3.08	<0.0001
Soil \times Species	1	4.802	13.58	>0.05
Habitat \times Species \times <i>B. diandrus</i> density	1	1.683	4.63	<0.001
Error	95	0.3635		<0.05

indicates that interspecific competitive suppression of *B. hordeaceus* by *B. diandrus* was more strongly expressed under oak canopy than in open grassland habitat (Fig. 7).

DISCUSSION

Distribution patterns and population processes—A primary goal of this study was to use field experiments to assess

the interactive influence of congeneric competition and other environmental factors in creating observed shifts in *Bromus* species dominance between open grassland and oak canopy understory. If population processes are involved in creating these shifts in distribution, one would expect fitness param-

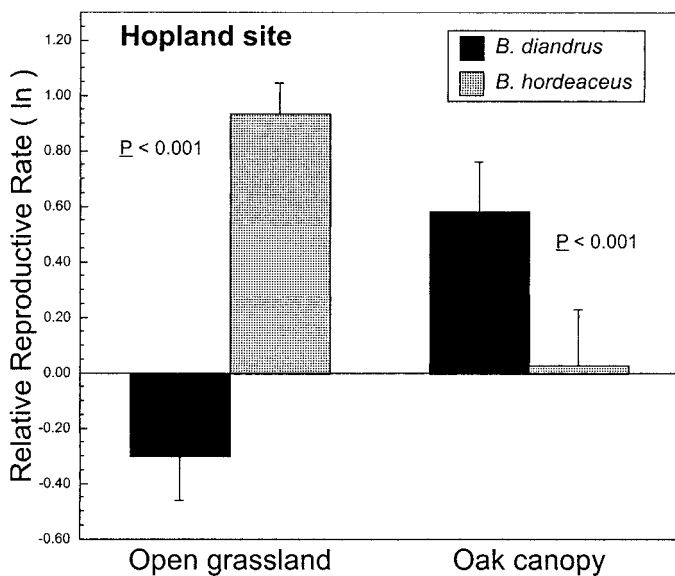


Fig. 4. Differential effects of habitat type (open grassland vs. under oak canopy) on relative reproductive rate (means \pm 1 SE) in *B. hordeaceus* and *B. diandrus* populations at the Hopland site. Relative reproductive rate was estimated by dividing seed output per plot by seed input (i.e., planting density per plot). Significance levels are for differences between species within a habitat.

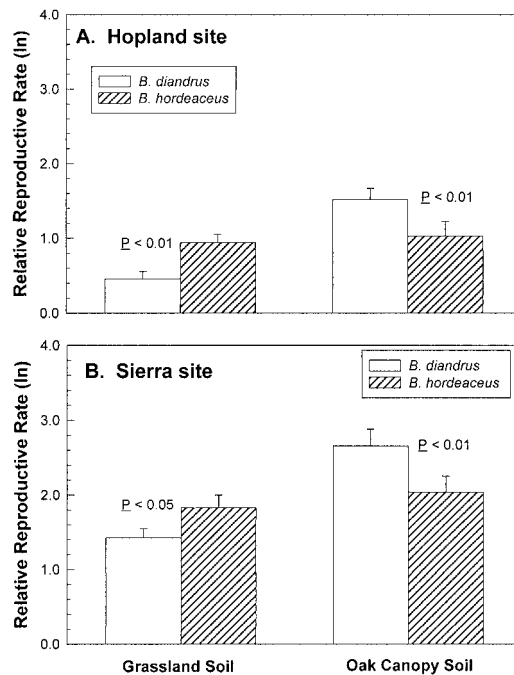


Fig. 5. Differential effects of soil type on relative reproductive rates (means \pm 1 SE) of *B. hordeaceus* and *B. diandrus* populations at (A) the Hopland site and (B) the Sierra site. Significance levels are for differences between species within a soil type.

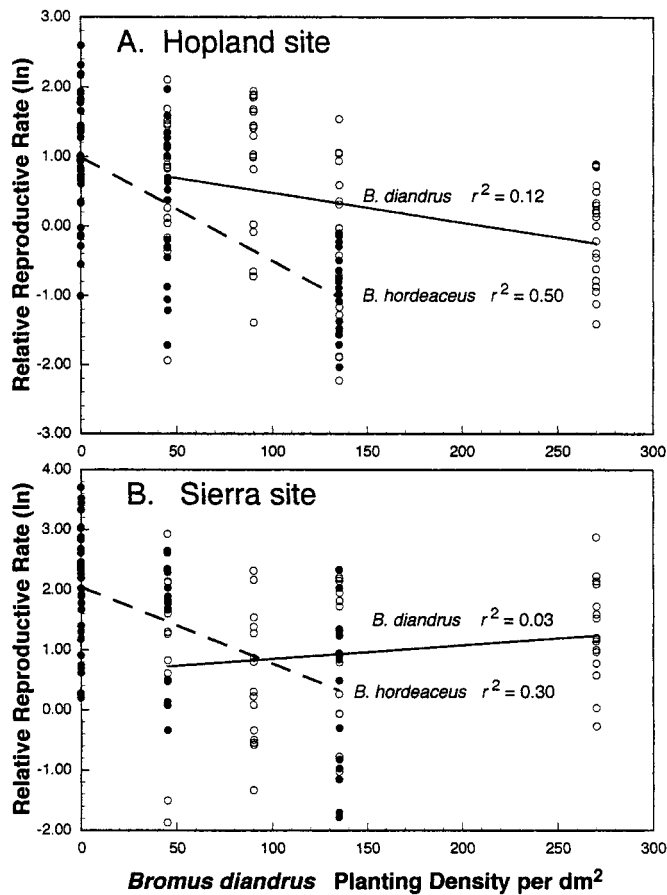


Fig. 6. Effects of *B. diandrus* density variation on relative reproductive rates of *Bromus* populations at (A) the Hopland site and (B) the Sierra site.

ters to exhibit some sort of crossing interaction of species and habitat, such that the demographic performance for a species is highest in the habitat where it is dominant. In general, these fitness crossing interactions were found to exist in the direction predicted from the species' distribution in the field. The measurements taken along transects at the Hopland field site indicated that *B. hordeaceus* is much more abundant in open grassland, while *B. diandrus* clearly dominates under oak canopy. The species by habitat interactions in demography measured at the Hopland field site would predict this distribution pattern; population growth rates as measured by RRR were higher for *B. hordeaceus* in the grassland, while *B. diandrus* exhibited higher RRR under oak canopy. At the Sierra field site, observed shifts in the field distributions of *B. hordeaceus* were not as pronounced, suggesting that *B. diandrus* dominance of the canopy habitat was not as strong. In their study on effects of rainfall on understory production and composition, McClaran and Bartolome (1989) also found that *B. hordeaceus* was relatively more abundant under canopy at Sierra than at the other four sites they examined. This weaker gradient in species distribution at Sierra parallels the weaker species by habitat interactions in demographic performance measured at this site. Significant crossing interactions between habitat and species were not detected for RRR at the Sierra site. However, significant three-way interactions among habitat, species, and *B. diandrus* density still indicate a relative advantage for *B. diandrus* under canopy and a slight advantage

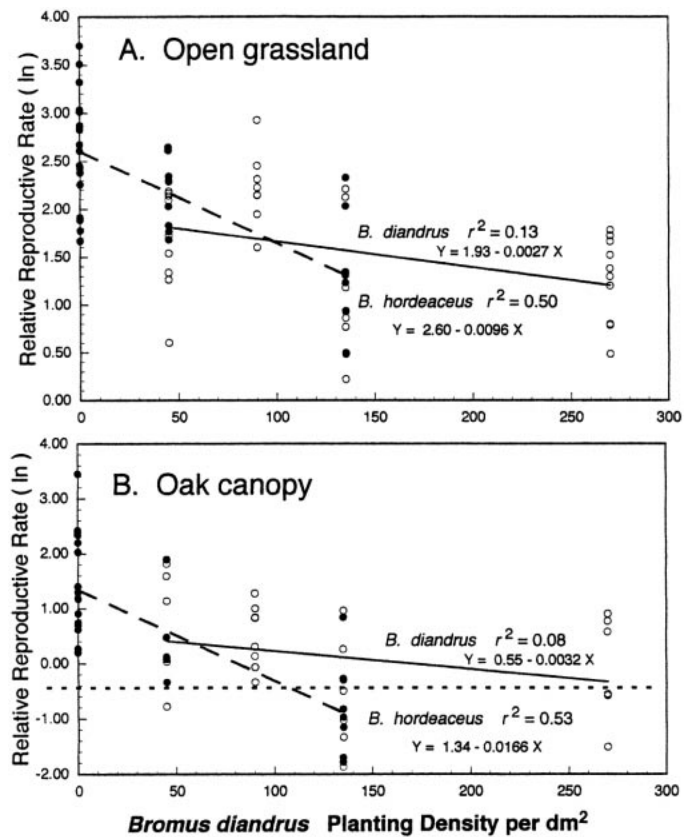


Fig. 7. Three-way interaction indicating that the effect of *B. diandrus* density variation on *B. hordeaceus* population growth at the Sierra field site varied between (A) open grassland and (B) oak canopy habitats.

for *B. hordeaceus* in open grassland. In a sense, the evidence from the Sierra site is negative; however, the results are still consistent with a population-based explanation for the shifts in distribution of the two species. The weaker gradient in species dominance between grassland and oak understory measured at Sierra would be predicted from the weaker interaction between species and habitat in demographic performance.

Competition and species distribution—An important question is whether interspecific competition between the congeners could contribute to the observed species distribution gradient. In their review of field competition experiments, Goldberg and Barton (1992) noted that a proper test of the importance of interspecific competition in affecting distribution patterns requires the examination of the interaction of habitat, target species and competitive interaction (hereafter referred to as the competition by habitat interaction). They argue that for a conclusive demonstration of the importance of interspecific competition in affecting the distribution of a species, the competition by habitat interaction should indicate that: (1) interspecific competition reduces a species performance most in a habitat where the species does not normally occur; and, (2) in habitats where it does not normally occur, the reduction in performance is greater for this species than for another species that normally occurs in the habitat. At both the Hopland and Sierra sites, *B. diandrus* was a stronger interspecific competitor than *B. hordeaceus*. However, it is only at the Sierra site that the effect of interspecific competition from *B. diandrus* ap-

pears to vary with habitat (Fig. 7). With increasing *B. diandrus* density, *B. hordeaceus* population growth decreases more rapidly under oak canopy (ANCOVA, $P < 0.05$; regression slope = -0.0166) than in the grassland plots where it is more common (slope = -0.0096). Thus for estimates of population growth in *B. hordeaceus*, the first competition criterion noted by Goldberg and Barton (1992) is satisfied because negative interspecific competitive effects on *B. hordeaceus* are most pronounced in the site where this species is in low abundance (i.e., under oak canopy). Next it is necessary to demonstrate that, under oak canopy where *B. diandrus* is dominant, interspecific competition has a stronger effect on *B. hordeaceus* than on *B. diandrus*. This condition is supported by the general results indicating that *B. diandrus* is the stronger interspecific competitor regardless of habitat type. Variation in *B. diandrus* density has a highly significant effect overall on *B. hordeaceus* population growth rates ($P < 0.001$; Table 3), while variation in *B. hordeaceus* density does not significantly affect population growth rates in *B. diandrus* ($P > 0.20$; Table 3). Thus, it appears that the distribution of *B. hordeaceus* could be significantly influenced by interspecific competition from its congener, *B. diandrus*. However, this does not appear to be the case for *B. diandrus* because, as noted above, variation in *B. hordeaceus* density did not have a significant effect on population growth rates in *B. diandrus*. The relative insensitivity of *B. diandrus* to density variation in *B. hordeaceus* suggest that interspecific competition from *B. hordeaceus* is not an important factor in determining distribution patterns of *B. diandrus*. In this reversal of species dominance from grassland to oak understory, interspecific competition between these two species may affect distribution patterns of the grassland dominant only. Larger individual seed mass in *B. diandrus* may contribute to its apparent competitive superiority to *B. hordeaceus*. Both theoretical (Geritz, 1995; Rees and Westoby, 1997) and empirical studies of annuals (Mack and Harper, 1977; Law and Watkinson, 1987; Turnbull, Rees, and Crawley, 1999) have demonstrated repeatedly that increased seed mass is correlated with increased competitive ability.

The fact that the competition by habitat interaction was not significant at the Hopland site suggests that the effect of interspecific competition on the distribution of these annuals may vary spatially or temporally, or both. Unfortunately, spatial and temporal effects on the competition by habitat interaction cannot be separated in this study because the experiments at each field site were also conducted during different years. We are not aware of other studies that have looked at spatial or temporal variation in the occurrence of competition by habitat interactions (Goldberg and Barton, 1992), so it is unknown whether our results can be generalized to other systems. Whether competition occurs at all often seems to be dependent on spatial and temporal variation (Goldberg and Barton, 1992), so it seems a reasonable extrapolation to expect that these more complex interactions involving competition might also be environment dependent.

Finally, it is possible that the nonsignificance of the competition by habitat interaction at the Hopland site may result from intraspecific genetic differences between populations of the two *Bromus* species at the two field sites. Previous work on *B. hordeaceus* in California has demonstrated that there is significant variation among populations of this species in growth and demographic response to both intra- and interspecific competition (Wu and Jain, 1979). Because we only used locally collected seeds of both species at each site, we cannot

use our results to test for this possibility. It should be noted, however, that at both Hopland and Sierra, *B. diandrus* was consistently insensitive to interspecific competition from its congener, while *B. hordeaceus* was strongly suppressed by increasing *B. diandrus* density.

With regard to the role of competition in affecting species distribution, the study by Maranon and Bartolome (1993) on vegetation shifts under the evergreen oak *Quercus agrifolia* provides an interesting contrast to our study conducted under deciduous oak canopy. They argued convincingly that because deep shade under a dense evergreen oak canopy reduces herbaceous cover to such a low level, interference among herbaceous species should be very weak. As a result, they suggested that competitive effects of understory species such as *B. diandrus* are not important in suppressing populations of open grassland species such as *B. hordeaceus* under evergreen canopy. In contrast, our results indicate that interspecific competition from *B. diandrus* is likely an important factor reducing the abundance of *B. hordeaceus* under blue oak canopy. We suggest that our contrasting results reflect the greater light availability and resulting higher plant density under deciduous oaks compared to evergreen oaks (Holland, 1973). For example, the plant density measured by Maranon and Bartolome (1993) under dense evergreen canopy was much lower (10 plants/dm²) than the density gradient we used in our experimental treatments (i.e., 45–270 seeds/dm²).

The demographic results from the Sierra site provided evidence for the importance of competition from *B. diandrus* in determining the distribution of *B. hordeaceus*. In contrast, *B. diandrus* was found to be relatively insensitive to interspecific competitive effects from its congener either under canopy or in open grassland. This raises the question as to what factors reduce population growth of *B. diandrus* in open grassland (Fig. 4) and thus contribute to its lower abundance in this habitat (Table 3).

Our data on nutrient levels under canopy indicate significantly higher levels of both N and P relative to the open grassland at both Hopland and Sierra (Table 4). Because reduced soil fertility in grassland soils decreased the population growth of *B. diandrus* to a greater extent than in *B. hordeaceus* at both sites (Fig. 5), we propose that this gradient in soil fertility between the two habitats helps to explain the lower abundance of *B. diandrus* in less fertile open grasslands. Our results agree with previous studies that have indicated that *B. diandrus* responds favorably to increased nutrient availability (Jones and Evans, 1960; Jones and Winans, 1967; Hull and Muller, 1976; Heady et al., 1992). As part of their study on the distribution of *B. diandrus* and *A. fatua* beneath coast live oaks, Parker and Muller (1982) examined the effects of soil nutrients on both grass species. Their results indicated that *B. diandrus* was more responsive than *A. fatua* to the higher nutrient status associated with soils under canopy, especially under shaded conditions. They thus concluded that soil fertility gradients contributed, at least in part, to the dominance of *B. diandrus* under live oak. Similarly, higher soil nutrient levels under blue oak canopy were also found by Holland (1973). Although Holland did not conduct any experiments, he suggested that increased cover by *B. diandrus* under canopy resulted from soil nutrient differences.

In sum, we suggest that factors determining the relative abundance of these two bromegrasses along the environmental gradient between open grassland and oak understory may be different for each species. The grassland dominant *B. hordea-*

ceus appears to be restricted in its distribution by competition from its congener, the oak canopy dominant *B. diandrus*. In contrast, *B. diandrus* is largely unaffected by interspecific competition from *B. hordeaceus*. It is possible that competition from other species that are common in the open grassland but relatively rare under canopy may act to reduce *B. diandrus* abundance in open grassland. For example, competition from *Erodium cicutarium*, a species absent from the understory but abundant in open grassland, may affect *B. diandrus* distribution. Similarly, Maranon and Bartolome (1993) argued that dominant tall grasses such as *Avena fatua* might limit establishment of understory species such as *B. diandrus* in open grassland. Although competition from other species like *Erodium* or *Avena* may play a part in reducing *B. diandrus* abundance in open grassland, it is important to note that we measured reduced growth for open grassland populations of *B. diandrus* populations within an experimental design that strongly reduced potential competition from such species. As a result, we suggest that physical conditions in the open grassland might be just as important as competition from grassland dominants in reducing *B. diandrus* population growth. In particular, our results from the soil reciprocal transplant treatments indicate that reduced nutrient availability found in open grassland sites may limit the abundance of *B. diandrus* in this habitat.

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