

Variation in the establishment of a non-native annual grass influences competitive interactions with Mojave Desert perennials

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Abstract Competition between native and non-native species can change the composition and structure of plant communities, but in deserts, the highly variable timing of resource availability also influences non-native plant establishment, thus modulating their impacts on native species. In a field experiment, we varied densities of the non-native annual grass *Bromus madritensis* ssp. *rubens* around individuals of three native Mojave Desert perennials—*Larrea tridentata*, *Achnatherum hymenoides*, and *Pleuraphis rigida*—in either winter or spring. For comparison, additional plots were prepared for the same perennial species and seasons, but with a mixture of native annual species as neighbors. Growth of perennials declined when *Bromus* was established in winter because *Bromus* stands had 2–3 months of growth

and high water use before perennial growth began. However, water potentials for the perennials were not significantly reduced, suggesting that direct competition for water may not be the major mechanism driving reduced perennial growth. The impact of *Bromus* on *Larrea* was lower than for the two perennial grasses, likely because *Larrea* maintains low growth rates throughout the year, even after *Bromus* has completed its life cycle. This result contrasts with the perennial grasses, whose phenology completely overlaps with (*Achnatherum*) or closely follows (*Pleuraphis*) that of *Bromus*. In comparison, *Bromus* plants established in spring were smaller than those established in winter and thus did not effectively reduce growth of the perennials. Growth of perennials with mixed annuals as neighbors also did not differ from those with *Bromus* neighbors of equivalent biomass, but stands of these native annuals did not achieve the high biomass of *Bromus* stands that were necessary to reduce perennial growth. Seed dormancy and narrow requirements for seedling survivorship of native annuals produce densities and biomass lower than those achieved by *Bromus*; thus, impacts of native Mojave Desert annuals on perennials are expected to be lower than those of *Bromus*.

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Introduction

Non-native annual grasses have threatened arid plant communities in western North America since their introduction and subsequent expansion during the past century (Mack 1981; Billings 1990; Vitousek 1990; D'Antonio and Vitousek 1992; Salo 2005). In the Mojave Desert, abundant shoot production coincides with above-average winter and spring rainfall (Hunter 1991). Consequently when these non-native plants senesce, persistent shoots create fuel for wildfires, which injure or eliminate native perennials that are poorly adapted to repeated burning (Beatley 1966; McLaughlin and Bowers 1982; Brown and Minnich 1986; Rogers and Vint 1987; Billings 1990). Despite localized portions of the southwestern hot desert region that have been impacted by wildfire (Brooks and Minnich, in press), the consequences of the widespread occurrence of non-native grasses in unburned shrublands are unknown. Specifically, it is unclear whether non-native annual species compete with and negatively impact native desert perennials or if non-native annuals and native perennials coexist because perennials are adapted to extreme and variable desert conditions.

With rising demands on controlling and eradicating a large number of invading species, it is necessary to assess the impact of non-native species by determining their range, abundance and effect on native species (Parker et al. 1999). The range and abundance of *Bromus madritensis* ssp. *rubens* (red brome) are well documented: this non-native annual grass species is now widespread throughout the Mojave Desert (Beatley 1966; Hunter 1991; Brooks 1999a; DeFalco et al. 2001; Salo 2005) and can comprise a large proportion of the total annual plant production (Beatley 1969; Hunter 1991; Brooks 2000; DeFalco et al. 2001). Yet, its effect, defined as the per-capita or per-biomass influence on native species, is poorly understood. Although the potential for invasive non-native annuals to reduce the performance of perennials is recognized (Harris 1967; Melgoza et al. 1990; Melgoza and Nowak 1991; Dyer and Rice 1999; Holzapfel and Mahall 1999; Brown and Rice 2000), few mechanistic studies have specifically examined the interac-

tions between *Bromus madritensis* ssp. *rubens* (hereafter referred to as *Bromus*) and perennial species whose resources they share, or determined how the effects of *Bromus* on native species differ from those of native winter annuals.

Native perennial species that dominate desert communities are adapted to capture soil water when it becomes available or to use water efficiently when soil moisture is in short supply. In contrast, germination and growth of winter annuals typically coincide with favorable growth temperatures and soil moisture recharge from winter rainfall (Beatley 1974). When winter rainfall is scarce, however, germination of Mojave Desert annuals may correspond with early spring rainfall, although usually in lower densities and biomass (Beatley 1974). Like native annuals, *Bromus* germinates in either winter or spring, depending on rainfall, and both *Bromus* and the native annuals predominantly establish beneath the canopies of perennial species (Samson 1986; Brooks 1999b). Early and rapid carbon gain by annuals occurs at the expense of great water loss, which may allow annual species (both native and non-native) to exploit soil water normally used by shrubs and perennial grasses. The similar establishment and shared life history strategy of *Bromus* and native annuals suggest that these species may have similar effects on perennials. However, *Bromus* can deplete soil resources such as water and N more rapidly than native winter annuals (DeFalco et al. 2003). Consequently, performance of perennials with neighbors comprised primarily of *Bromus* should decline more than if the neighbors are a mixture of native annual species. Furthermore, annuals that establish in the winter may have a greater impact on perennial plant performance than annuals that establish in the spring as earlier growth and resource use occurs before perennials become active. Thus, the variable timing of rainfall as well as the composition of the neighboring annual community likely affect the competitive relationship between annual and perennial plants in the Mojave Desert, but has not been previously studied.

Our first objective was to determine whether different times of establishment for *Bromus*—winter versus spring—influence its competitive effect on perennials. Emergence of a

similar non-native annual grass, *B. tectorum*, is variable in semi-arid regions of western North America (Anderson 1996) and consequently, competition with perennials is more intense when *B. tectorum* emerges early compared with those that emerge later (Blackshaw 1993). In our field study, *Bromus*' competitive effect was imposed in winter and spring by establishing different densities of *Bromus* around perennials using an additive design to determine whether neighboring *Bromus* plants reduce the growth and reproduction of the perennial species. We also sought to understand whether competition for water was the primary factor mediating these interactions.

Our second objective of this study was to determine whether competition with annuals varies among perennial growth forms. The net effect of the interactions between annual and perennial species depends not only on resource depletion by annuals, but also on the ability of the perennial species to persist when resources are depleted (Goldberg 1990; Goldberg and Landa 1991). We tested competition between *Bromus* and three perennial species that differ in phenologies and rooting depths. We expected the evergreen shrub *Larrea tridentata* to be less sensitive to neighboring annuals because *Larrea* can photosynthesize and grow at soil water potentials well below those tolerated by winter annuals (Smith et al. 1997). Furthermore, root systems of annuals typically occur in shallow soil depths (Cable 1969; Forseth et al. 1984), and thus annuals should have little effect on *Larrea*, whose root system allows it to take advantage of soil moisture at a greater lateral and vertical extent than neighboring annual plants (Gile et al. 1998). In contrast, we expected annuals to reduce the performance of perennial grasses because of their similar phenologies and rooting depths. For example, the activity of the perennial grass *Achnatherum hymenoides* overlaps completely with annuals (Nowak et al. 2001; DeFalco 2003), and thus competition with annuals for the same available soil water will likely reduce the growth of *Achnatherum*. Optimal temperatures for growth of *Pleuraphis rigida* occur after the annuals have completed most of their development (Nobel 1980). In addition, *Pleuraphis* carbon uptake is dependent on favorable soil

water potentials (Nobel 1980; Nobel and Zhang 1997). Thus, if annuals have extracted most of the available soil moisture before *Pleuraphis* is active, then little water will be available for *Pleuraphis* because of the pronounced late-spring/summer dry season.

Finally, we examined whether the competitive effect of *Bromus* on perennials will be greater compared to that of a mixture of native annual species. For comparison with *Bromus*' effects on perennial growth and reproduction, a mixture of native annual species was also established around a subset of plots with the same perennial species. Collectively, the objectives determine whether the impact of the non-native annual grass *Bromus madritensis* ssp. *rubens* varies across years, as influenced by the prevailing pattern of annual rainfall. Second, these data are important in determining whether some native perennial species are more resistant to the competitive effects of this non-native grass. Third, these objectives discern whether annual plants, regardless of their origin, are functionally similar in their impact on plant communities through competition, or if non-native species have unique traits that confer greater competitive effects, traits which in turn can help managers prioritize their eradication.

Materials and methods

Study area, perennial species and treatments

This study began in October 1999 and ended in June 2000 at Frenchman Flat, which is located at the Nevada Test Site (US Department of Energy) in southern Nevada, USA. Frenchman Flat represents an area of the Mojave Desert where *Bromus* has successfully invaded, as evidenced by *Bromus* densities at nearby sites having surpassed those of native annual species in recent decades (Hunter 1991; DeFalco et al. unpublished data). Three native Mojave Desert perennial species were selected for study: creosote bush, *Larrea tridentata* (DC.) Cov.; Indian ricegrass, *Achnatherum hymenoides* (Roemer & Schultes) Barkworth; and galleta grass, *Pleuraphis rigida* Thurber. Each individual perennial plant plus the area 20 cm beyond the canopy edge of the

perennial defined an individual study plot. Treatments were stratified among individual plots according to perennial plant volume, which was estimated as an inverted cone using each plant's canopy dimensions and height. Each individual perennial was randomly assigned a season for neighboring annual plant establishment (winter or spring) and a neighboring plant density (approximately 0, 200, 400, 600, 800 or 1000 individuals m^{-2}). To minimize competition from neighboring perennials, perennial vegetation within a 2 m radius of each *Larrea*, *Achnatherum*, and *Pleuraphis* individual was clipped to just below the crown.

For the winter establishment treatment, *Bromus* seeds previously collected from the area were hand broadcast on each plot on November 9 and 10, 1999 (i.e., beneath each individual perennial plant and out to an area 20 cm beyond the canopy edge). A light layer of straw mulch was placed on top of all plots (both the seeded winter establishment plots as well as the unseeded spring establishment plots) and secured in place with commercially available nylon bird netting. On February 9 and 10, 2000, straw and mesh were lifted from the spring establishment treatments, *Bromus* seed was sown as on winter treatment plots, and straw and mesh replaced. The winter establishment treatment was irrigated with 25 mm water approximately once every 1 to 2 weeks with a cyclone circular sprinkler, starting on November 11, 1999 and continuing until January 8, 2000. For the spring establishment treatment, irrigation occurred at the same rate as the winter treatment from February 11, 2000 until March 24, 2000. Straw from winter and spring plots was removed after irrigation ceased, and annual seedlings were established. A total of 72 plots were established that had a single perennial plant with neighboring *Bromus* plants (3 perennial species \times 2 seasons of establishment \times 6 planting densities \times 2 replicates per treatment combination).

Twenty-four additional plots were similarly prepared but with neighboring annuals composed of a mixture of native species. For these native annual plots, seed trapped in litter beneath nearby *Larrea* canopies was collected and spread around all individuals of the three perennial

species and irrigated in a manner similar to the *Bromus* plots. Thus, the overall experimental design was similar to that of the *Bromus* plots (3 perennial species \times 2 seasons of establishment), but with 4 replicates per treatment combination and no density manipulation.

For the *Bromus* treatments, annuals were thinned up to 1 month after germination in an attempt to maintain the density and composition of the neighboring annual plants at the desired treatment levels. *Bromus* was thinned to approximate the target density by clipping plants at ground level, and any native annual species were similarly removed. For the perennials with neighboring plants of a mixture of native annual species, *Bromus* was removed but the native densities were not manipulated.

Shoots of neighboring annual plants were harvested when they senesced in late April and early May, sorted by species, and dried at 60°C to a constant mass. Plots with *Bromus* as the neighbor treatment had on average $\geq 85\%$ *Bromus* by mass; the remaining biomass included native plants that germinated after thinning was completed. However, one plot each with *Pleuraphis* and *Larrea* had $< 85\%$ of *Bromus* neighbors, and these plots were omitted from analyses. Biomass of native annuals for the mixed species plots averaged $\geq 85\%$, with *Bromus* comprising the remaining biomass; thus, none of the mixed treatment plots were eliminated from analyses.

Soil water status

Volumetric soil water content (θ_{vol}) was monitored for each plot throughout the study. An aluminum tube (41 mm outer diameter, 39 mm inner diameter) was placed vertically in the ground to a depth of 135 cm and at 10 cm from the canopy edge of each perennial. θ_{vol} was measured monthly at 15, 35, 55, 75, 95, 115 and 135 cm depths using a calibrated neutron probe soil moisture device (Hydroprobe Moisture Depth Gauge, Campbell Pacific Nuclear, Martinez, California, USA). These measurements were used to calculate soil profile moisture (mm) according to Yoder and Nowak (1999) as in Anderson et al. (1993). We assumed deep drainage was negligible because θ_{vol} did not change significantly below 75 cm throughout the

duration of the study. We also assumed run-on and run-off were insignificant because the plots were situated far apart on a topographically flat area, and we observed no lateral surface movement of water when irrigation was applied. Thus, water use (mm) was based on calculating evapotranspiration using a modified water balance equation: water use = precipitation + irrigation – Δ soil storage.

Seasonal growth, reproduction and water potentials of perennials

Shoot relative growth rates (RGR) of the individual perennials were determined by monitoring plant growth monthly beginning when plants were dormant in November and ending when plants senesced by June. For *Achnatherum* and *Pleuraphis*, two tillers were selected per plant and tagged at the base with a loose band of colored tape. The length of each leaf per tiller was measured at each sampling time. The relationship between leaf length and leaf mass was determined using leaves harvested from plants close to the experimental plants; this relationship was used to estimate the total leaf biomass on each tiller every time measurements were collected. For *Larrea*, four terminal twigs, each approximately 2 cm long, were tagged with tape. Twig length and the number of leaflet pairs were measured at each sampling time. Similar to the grasses, twig mass was estimated from twigs harvested from *Larrea* plants adjacent to the study plots. Because we wanted to examine the effect of neighboring annuals on growth of perennials, tiller and twig RGR were calculated from the time neighboring annuals were seeded (November for winter establishment treatments and February for spring) until perennials reached peak production (late April to late May). RGR was calculated according to Blackman (1919) and used the tiller or twig means of the \log_e -transformed masses to avoid bias in the estimates (Hoffmann and Poorter 2002). Growth of three *Larrea* individuals was difficult to measure because bagworms (*Thyridopteryx meadi*) altered the lengths of twigs and used leaflets for constructing cocoons; these *Larrea* individuals were omitted from analyses.

Flowers produced on the marked grass tillers and *Larrea* twigs were counted at each sampling time. Reproductive effort (RE) at peak flower production for each perennial was calculated as the ratio of the average number of flowers to the corresponding average production (g) among twigs or tillers.

Pre-dawn (Ψ_{pre}) and mid-day (Ψ_{mid}) water potentials were measured on individual perennials at peak production (April 15 for winter treatment and April 29 for spring treatment). A single terminal twig for *Larrea* and the most-recently fully expanded leaf for *Achnatherum* and *Pleuraphis* were selected for each plant and each measurement, but tissues were not sampled on the same branches or tillers that were used for growth. Water potentials were measured by excising the plant tissue and placing it in a Scholander-type pressure chamber (PMS Instrument Co., Corvallis, Oregon).

Statistical analyses

Profile soil moisture was analyzed in separate fixed effects ANOVAs (perennial species \times season of establishment) before irrigation, at the onset of perennial growth, and after *Bromus* senesced. The relationship between neighbor plant biomass and neighbor plant density was linearized by \log_{10} -transforming both variables and then tested in ANCOVA with neighbor identity (*Bromus* versus mixed species) and season of establishment (winter versus spring) as qualitative variables and neighbor density as a quantitative variable expressed through a linear term (Fernandez 2001). SAS statistical software (SAS Institute, Cary, NC, version 8) was used to perform all statistical analyses.

Analysis of competition was conducted in two steps: the first step tested whether the relationship between perennial responses (RGR, RE, water use, and water potential) and *Bromus* neighbor biomass was the same between seasons and among perennial species (tests of homogeneity of slopes), and the second step tested whether mixed native annuals had the same effect on perennial responses as *Bromus* neighbors (diagnostic tests for outliers). In the first step, analysis of competition between

perennials and annuals was based on the stepwise ANCOVA model for field competition experiments described by Goldberg and Scheiner (2001) and performed using SAS macro applications (Fernandez 2001). Only the *Bromus* neighbor plots were included to determine if perennial responses significantly changed with an increase in *Bromus* biomass (quantitative factor) and whether this relationship differed among perennial species and between the seasons of establishment (qualitative factors). All statistical models tested linear and quadratic effects. Equal variance assumption was determined from residual plots, and when violated (i.e., RE), data were \log_{10} -transformed before analysis (Box and Cox 1964).

The range of biomass values for the *Bromus* plots often did not include the range of biomass values for the mixed species plots, in part because fewer plots were prepared with mixed annual species compared with *Bromus* plots. Thus, comparison between mixed annual and *Bromus* effects by adding neighbor identity as a qualitative factor in an ANCOVA is inappropriate (Quinn and Keough 2002). Consequently, in the second step of statistical analysis, we used outlier detection diagnostics to determine whether responses of perennials with mixed species neighbors deviated significantly from those with *Bromus* neighbors. This ANCOVA included all the data (i.e., *Bromus* and mixed species plots) with season and perennial species as qualitative factors, and biomass of the annual neighbor—regardless of whether it was *Bromus* or mixed species—as the quantitative factor. We expected that mixed species neighbors would have less per-biomass impact on perennials than *Bromus* neighbors, and therefore mixed species plots would be detected as significant outliers from the fitted regression. Based on examination of studentized residuals, normal probability plots, and according to D'Agostino (1971), outliers were identified and then iteratively removed.

Results

The experiment occurred during a dry hydrological year (October 1999 through September 2000), which had 76% of the long-term mean annual

rainfall. The total water added by irrigation and rainfall during the irrigation period was similar for both seasons of annual establishment (148 mm for winter and 147 mm for spring). Because rain events occurred after the irrigation period, total moisture input through May was 208 mm for the winter and 155 mm for the spring annual establishment treatments. Although direct comparisons between the amounts of sprinkler-applied water and rainfall are confounded by differences in intensity and duration of events as well as by evaporative conditions during and immediately after the event, the total moisture inputs for the annual establishment treatments were substantially greater than the average long-term October through May precipitation for the area (90 mm), but were similar to the amount recorded during October 1997 through May 1998 (195 mm), which was a wet El Niño year.

Annuals germinated soon after water was applied. Annuals that were seeded in winter germinated, developed, and produced seed, and then senesced within 25 weeks whereas those seeded in spring completed their life cycle within 13 weeks. Annual plants senesced in late April to early May regardless of the time they were seeded. In comparison, perennial plant phenology was neither consistently influenced by irrigation nor synchronized with the establishment of neighboring annuals.

Because the different timing of irrigation confounds seasonal comparisons of soil water content on the same date, comparisons of soil moisture were made at three similar phenological stages. Prior to initial irrigation, soil moisture measured on November 10 and January 27 for winter and spring annual establishment treatments, respectively, was lower for *Larrea* compared with the perennial grasses (species effect, Table 1). As may be expected, soil moisture was lower before irrigation in the spring establishment treatment compared with winter (season effect, Table 1) due to the 3-months lag between the two seasons when irrigation began. At the onset of perennial growth, soil moisture was higher in winter than in spring for *Achnatherum*, higher in spring than winter for *Larrea*, and the same in both seasons for *Pleuraphis* (species \times season interaction, Table 1). By the time *Bromus* senesced in late

Table 1 Profile soil water (mm, mean ± SE) to a depth of 1.35 m around three Mojave Desert perennial species measured at three different phenological stages

	<i>Achnatherum</i>	<i>Pleuraphis</i>	<i>Larrea</i>	Source	df	<i>P</i>
<i>Before irrigation</i>						
Winter	118 ± 1	119 ± 2	114 ± 2	Species	2, 55	0.02
Spring	110 ± 1	110 ± 1	107 ± 1	Season	1, 55	<0.01
				Species × Season	2, 55	0.77
<i>Onset of perennial growth</i>						
Winter	138 ± 3	156 ± 4	141 ± 7	Species	2, 58	<0.01
Spring	110 ± 1	153 ± 4	161 ± 5	Season	1, 58	0.28
				Species × Season	2, 58	<0.01
<i>After Bromus senescence</i>						
Winter	129 ± 5	131 ± 4	119 ± 3	Species	2, 60	0.03
Spring	124 ± 4	128 ± 5	118 ± 3	Season	1, 60	0.34
				Species × Season	2, 60	0.92

Factors in the ANOVA were perennial species (Species) and season of *Bromus* establishment (Season)

April to early May, soil moisture again was lowest for *Larrea* plots compared with those of the perennial grasses, and all species had depleted soil moisture similarly for the two seasons of annual plant establishment (Table 1).

Seasonal effect on production of annual neighbors

The positive relationship between annual plant biomass and density (after both axes were log₁₀-transformed) differed among the four different treatment combinations of annual species composition and season of annual establishment (density × species × season; Fig. 1, upper graph; Table 2). The slope of this relationship was lowest for the *Bromus*-winter and *Bromus*-spring treatments and greatest for the mixed annual-winter treatment (density × species). Nonetheless, mean biomass of *Bromus* was greater than that of the mixed annual species (species effect, Table 2), but greater densities of *Bromus* beneath perennials than mixed annual species also contributed to greater biomass for *Bromus* at both winter and spring establishment treatments compared with mixed annual species. Biomass of neighboring annuals was six times greater for plots established in winter than those in spring (season effect, Table 2) for both *Bromus* (45.1 ± 1.0 versus 7.2 ± 1.1 g m⁻²) and mixed annual species (9.4 ± 1.2 versus 1.6 ± 1.1 g m⁻²). Finally, a pronounced competition-density effect was observed for *Bromus* (i.e., large negative slopes for

the relationship between plant size and annual density, Fig. 1, lower graph) compared with mixed species (density × species, Table 2). Analyzed separately, biomass of individual *Bromus* plants decreased as density increased in the winter (log₁₀ – log₁₀ slope = –0.68, df = 1, 27, *P* < 0.01) and spring (log₁₀ – log₁₀ slope = –0.48, df = 1, 27, *P* < 0.01) establishment treatments, but biomass of individual plants for the mixed annual treatment was not affected by crowding in either season (winter log₁₀ – log₁₀ slope = 0.23, df = 1, 9, *P* = 0.20; spring = –0.40, df = 1, 11, *P* = 0.18).

Seasonal effect on competition between annual neighbors and perennials

Bromus had an overall negative effect on shoot relative growth rate (RGR) when the model was fitted without the mixed annual species treatment (biomass effect, Table 3). RGRs were significantly different among the three perennial species, with the grasses having the highest RGRs (*Achnatherum*, 0.018 ± 0.003 d⁻¹; *Pleuraphis*, 0.018 ± 0.002 d⁻¹) and *Larrea* the lowest (0.006 ± 0.003 d⁻¹). The slopes of the relationship between perennial RGR and *Bromus* biomass were significantly different among species at *P* = 0.06 (df = 2, 53; Fig. 2, upper graphs), with the grasses having more negative slopes (*Achnatherum*, –0.00022 d⁻¹ [g m⁻²]⁻¹; *Pleuraphis*, –0.00019 d⁻¹ [g m⁻²]⁻¹) than *Larrea* (–0.00007 d⁻¹ [g m⁻²]⁻¹). Although growth reflects measurements made on two tillers per individual

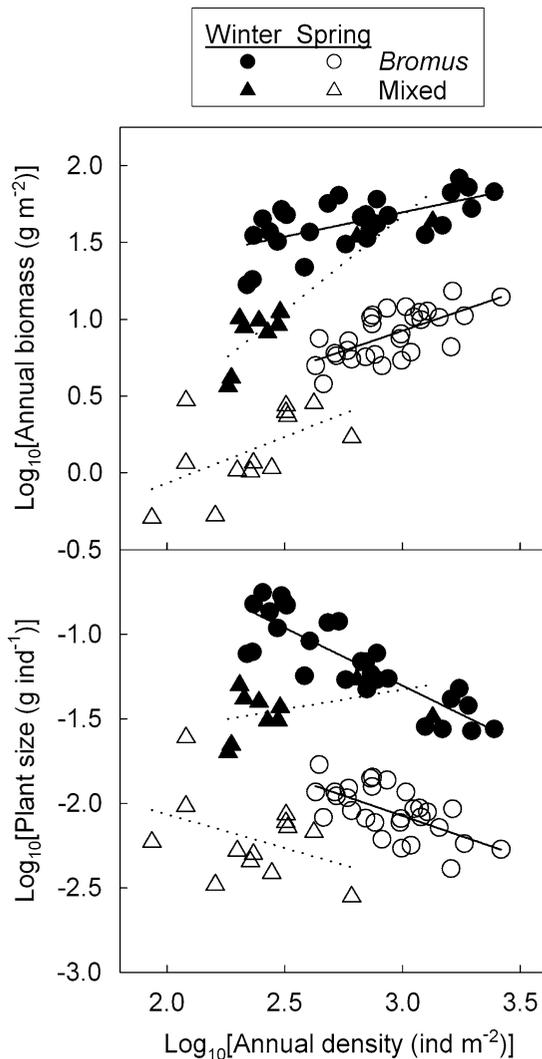


Fig. 1 Annual biomass (top) and plant size (bottom) as a function of plant density for the annual grass *Bromus* and mixed annual species that were established around perennials in winter or spring. Regression lines emphasize different slopes for *Bromus* (solid line) and mixed (dotted line) neighbors for winter and spring establishment treatments

perennial grass, the reductions in RGR with increased *Bromus* biomass were not offset by increases in the total number of tillers per perennial grass (data not shown). The effects of *Bromus* biomass on perennial RGR were not significantly different between the winter and spring establishment treatments (biomass \times season, Table 3). Nonetheless, stands of *Bromus* established in spring had lower biomass than those in winter, and consequently perennials with

neighboring *Bromus* plants that were established in spring had higher overall RGRs compared to those established in the winter ($0.018 \pm 0.003 \text{ d}^{-1}$ versus $0.010 \pm 0.001 \text{ d}^{-1}$, respectively; Table 3).

Reproductive effort for perennials with *Bromus* neighbors, measured as the number of flowers per g of production, did not vary with *Bromus* biomass or between seasons (Fig. 2, lower graphs). Averaged over neighbor biomass, RE was significantly lower for *Pleuraphis* with neighbors established in winter but was the same between seasons for both *Achnatherum* and *Larrea* (species \times season, Table 3).

The relative effects of the *Bromus* and mixed species treatments on perennial responses such as RGR and RE could not be compared using traditional ANCOVA because sample sizes for the mixed annuals were lower and the range of biomass for mixed annual treatments was smaller (and closer to zero) than those for *Bromus* (Fig. 2). Instead, we evaluated whether those perennials with the mixed species treatment were statistical outliers from the model fitted with both mixed species and *Bromus* treatments, which would suggest that perennials with neighbors of mixed annual species respond differently from those with neighbors of just *Bromus*. For perennial RGR, only two observations were outliers from the fitted model ($|\text{studentized residuals}| > 2.5$; D'Agostino Pearson Omnibus P -value < 0.01), and both observations were for *Pleuraphis* with the spring annual establishment treatment (Fig. 2). For these two outliers, one represented the *Bromus* neighbor treatment and the other represented the mixed annual species treatment. RE had no significant outliers. Thus, the effects of a mixture of annuals on perennial RGR and RE were quantitatively similar to those for *Bromus*.

Water relations

Total water use was greater for plots with annuals established in winter compared with those established in spring (Fig. 3). This greater water use was potentially influenced by the greater total water input as a result of rainfall that occurred after irrigation treatments were completed. Thus, to understand if the neighboring annual treat-

Table 2 Statistics for annual biomass and plant size with qualitative (neighbor species and season of establishment) and quantitative (annual density) factors

	df	Log ₁₀ [Biomass (g m ⁻²)]	Log ₁₀ [Size (g ind ⁻¹)]
		P	P
Density	1, 74	<0.01	<0.01
Species	1, 74	<0.01	<0.01
Season	1, 74	<0.01	<0.01
Species × Season	1, 74	0.70	0.74
Density × Species	1, 74	<0.01	<0.01
Density × Season	1, 74	0.81	0.74
Density × Species × Season	1, 74	0.01	<0.01

Axes for annual biomass and density were log₁₀-transformed before analysis

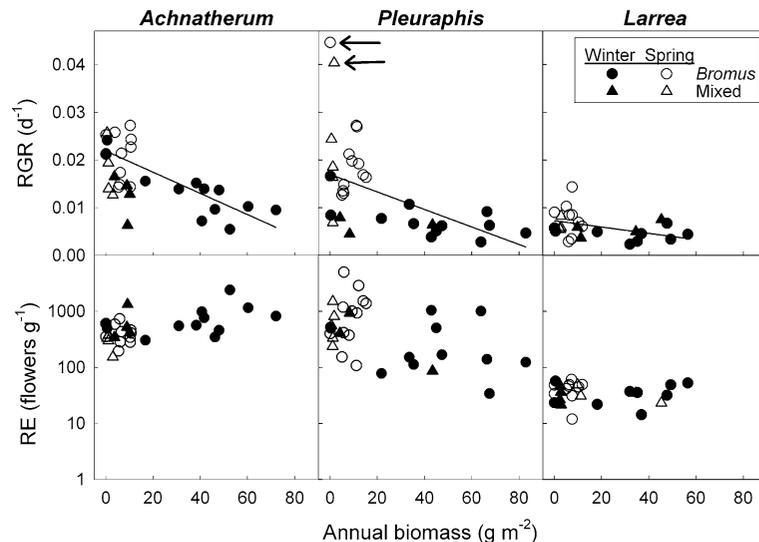
Table 3 Statistics for the ANCOVAs for perennial relative growth rate (RGR) and reproductive effort (RE) with qualitative (perennial species and season of establishment) and quantitative (*Bromus* biomass) factors

	df	RGR (d ⁻¹)	RE (flowers g ⁻¹)
		P	P
Biomass	1, 53	<0.01	0.72
Species	2, 53	<0.01	<0.01
Season	1, 53	<0.01	0.29
Species × Season	2, 53	0.02	<0.01
Biomass × Species	2, 53	0.06	0.29
Biomass × Season	1, 53	0.13	0.77
Biomass × Species × Season	2, 53	0.22	0.44

ments affected water use for the three Mojave Desert perennials, total water use was analyzed separately for the winter and spring treatments. The slopes of the relationship between total water use and *Bromus* biomass varied among the three perennial species when *Bromus* was established in the winter (biomass × species, Table 4). Water use for plots with *Pleuraphis* and *Larrea* increased as neighboring *Bromus* biomass increased (slopes = 0.33 mm [g m⁻²]⁻¹, df = 1, 10, P < 0.01 and 0.33 mm [g m⁻²]⁻¹, df = 1, 6, P = 0.04 for *Pleuraphis* and *Larrea*, respectively), but water use for plots with *Achnatherum* did not change with *Bromus* biomass (df = 1, 9, P = 0.88). In other words, an additional 3.3 mm of water was used over the growth season for every increase of 10 g m⁻² of neighbor *Bromus* biomass surrounding *Pleuraphis* and *Larrea* individuals. In contrast, total water use for the spring establishment treatment did not change with an increase in neighbor *Bromus* biomass, nor was it significantly different among perennial species (biomass × species and species effects, Table 4). To examine if total water use with mixed annuals was quantitatively different from that with just *Bromus* neighbors, we again examined the pooled model for statistical outliers. Only one plot, a *Larrea* with mixed annuals established in the spring, was a significant outlier.

Pre-dawn (Ψ_{pre}) and mid-day (Ψ_{mid}) water potentials of the three perennial species were more

Fig. 2 Relative growth rate (RGR; top) and reproductive effort (RE; bottom) for three perennial species as a function of biomass of *Bromus* or mixed annual species that were established in winter or spring. Regression lines represent a significant relationship between perennial RGR and *Bromus* biomass over both the winter and spring annual establishment treatments. Arrows point to statistical outliers



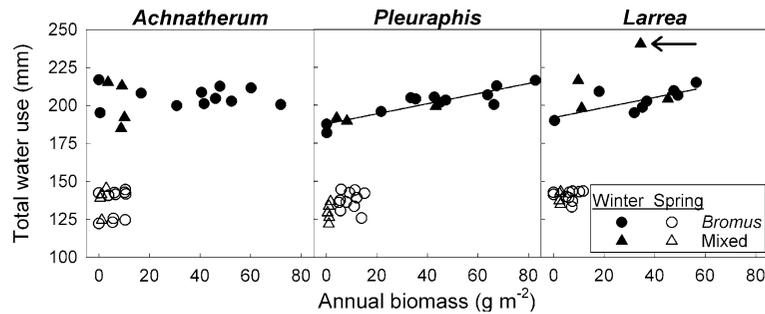


Fig. 3 Total water use for three perennial species as a function of biomass of *Bromus* or mixed annual species that were established in winter or spring. Regression lines represent a significant relationship between total water

Table 4 Statistics for separate seasonal ANCOVAs for perennial water use, and pre-dawn (Ψ_{pre}) and mid-day (Ψ_{mid}) water potentials with qualitative (perennial species) and quantitative (*Bromus* biomass) factors

	df	Water use	Ψ_{pre}	Ψ_{mid}
		(mm)	(MPa)	(MPa)
		<i>P</i>	<i>P</i>	<i>P</i>
<i>Winter treatment</i>				
Biomass	1, 26	<0.01	0.15	0.61
Species	2, 26	0.16	<0.01	<0.01
Biomass \times Species	2, 26	<0.01	0.35	0.35
<i>Spring treatment</i>				
Biomass	1, 26	0.64	0.85	0.41
Species	2, 26	0.26	0.48	0.05
Biomass \times Species	2, 26	0.68	0.21	0.38

negative for the spring annual establishment treatment than for the winter, but water potential did not vary with neighbor biomass (Table 4, Fig. 4). Among perennial species with *Bromus* neighbors only, Ψ_{pre} was significantly more negative for *Larrea* (-0.9 ± 0.1 MPa) than for either *Achnatherum* (-0.4 ± 0.1 MPa) or *Pleuraphis* (-0.5 ± 0.1 MPa) when neighboring *Bromus* plants were established in winter, but Ψ_{pre} was not significantly different among species when *Bromus* was established in spring. Ψ_{mid} was significantly lower for *Achnatherum* (-2.1 ± 0.1 MPa) and *Larrea* (-2.3 ± 0.1 MPa) than for *Pleuraphis* (-1.5 ± 0.1 MPa) when *Bromus* was established in winter, and was lower for *Larrea* (-3.2 ± 0.2 MPa) than for either *Achnatherum* (-2.7 ± 0.2 MPa) or *Pleuraphis* (-2.5 ± 0.1 MPa) when *Bromus* was established in spring. These differences in perennial plant water status between winter and spring

use and *Bromus* biomass over both the winter and spring annual establishment treatments. Arrow points to statistical outlier

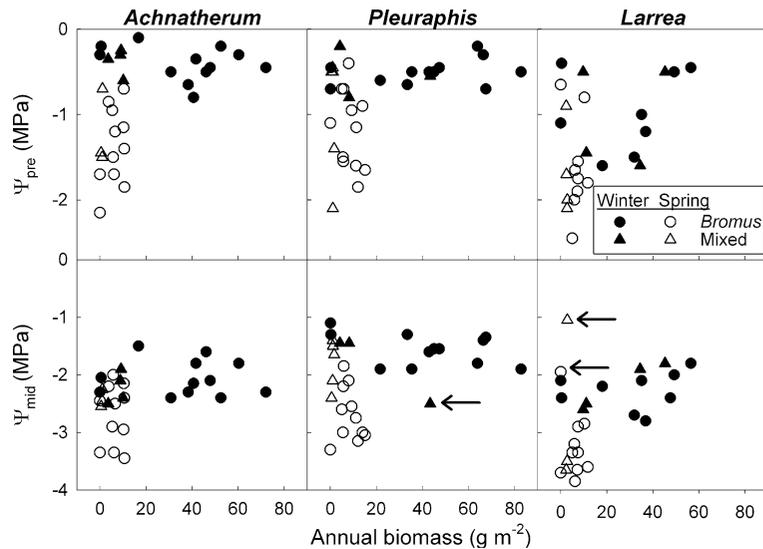
establishment of *Bromus* should be interpreted carefully—measurements were made at analogous phenological stages (i.e. at peak perennial production, which corresponded to April 15, 2000 for winter establishment treatments and April 29, 2000 for spring), but water status was also affected at least in part by the additional soil drying that occurred during the 2 weeks between the measurements.

Few statistical outliers occurred for water potentials when *Bromus* and mixed species treatments were considered together (Ψ_{mid} , Fig. 4). Only two of these outliers represented plots from the mixed species treatment, one established in spring for *Larrea* and the other established in winter for *Pleuraphis*.

Discussion

The non-native annual grass *Bromus madritensis* ssp. *rubens* reduced the growth of adult Mojave Desert perennials when *Bromus* individuals established during winter, which is also when native perennials were dormant, but had less effect in spring when germination and growth of *Bromus* were synchronous with perennial plant activity. *Bromus* germinated shortly after seeds were sown and irrigated beneath the canopies of perennials in both winter and spring, but growth of *Bromus* plants that established in winter preceded perennial plant growth by 2–3 months and resulted in greater *Bromus* biomass beneath canopies of the perennials and higher total water use. Thus, moisture delivered in winter resulted in

Fig. 4 Pre-dawn (Ψ_{pre} ; top graphs) and mid-day (Ψ_{mid} ; bottom graphs) water potentials for three perennial species as a function of biomass of *Bromus* or mixed annual species that were established in winter or spring. Arrows point to statistical outliers



earlier and greater growth of *Bromus* and subsequent depletion of soil resources (e.g., soil water, N, etc.) that would otherwise be used by perennial plants. In contrast, moisture delivered in spring was comparatively less effective, likely in part due to high evaporative losses at the time of irrigation: germination in spring resulted in low biomass of *Bromus* around the perennials and less competitive effect on RGR of native perennials. Additionally, perennials that were active during the time that annuals were seeded for the spring treatment may have interfered with annual plant germination and establishment, thus resulting in the low biomass of *Bromus* (Whitson and Koch 1998).

Despite the prominent increase in total water use when *Bromus* neighbors were established in winter, direct competition for water does not appear to be the major mechanism behind the observed differences in perennial responses to winter and spring treatments. Other studies in western North America have shown that water stress and reduced performance of perennials are associated with high water use by stands of non-native annual neighbors such as *Bromus tectorum* in the Great Basin (Melgoza et al. 1990; Melgoza and Nowak 1991; Booth et al. 2003), a mixed native and non-native annual community in the Mojave Desert that includes *Bromus madritensis* ssp. *rubens* and *Schismus barbatus* (Holzapfel and Mahall 1999), *Bromus* spp. and *Avena* spp. in

coastal sage scrub (Eliason and Allen 1997), and mixed annual grasses and forbs in oak woodlands on the western slope of Sierra Nevada (Schultz et al. 1955; Gordon et al. 1989; Gordon and Rice 1993, 2000; Welker et al. 1991). However, in this study plant water potentials of perennials did not significantly decrease as a function of neighbor *Bromus* biomass. Furthermore, the pattern of plant water potential for the perennials was contrary to expectations if water use was a major competitive mechanism—greater total water use when *Bromus* establishes in winter is expected to result in greater stress for perennial plants, but the observed plant water potentials for the perennials with the winter establishment treatment indicated less water stress. The pre-dawn plant water potentials imply that the perennial plants had access to ample soil water, even at peak shoot production. Indeed, the irrigation and rainfall that occurred during the annual plant establishment treatments exceeded average precipitation for the region, and evapotranspiration from the plots was commensurate with an above-average rainfall year (Yoder and Nowak 1999). Nonetheless, reduced perennial RGRs also may be a consequence of depletion of soil N by *Bromus*, as has been found for *Artemisia tridentata* grown in association with *Bromus tectorum* in the Great Basin (Booth et al. 2003). Although we did not measure the status of soil and plant tissue N, *Bromus* has the potential to acquire soil N more

rapidly than perennial species. For example, N-uptake by *Bromus* in a glasshouse experiment exceeded that of *Achnatherum* and *Pleuraphis*, especially with regard to *Bromus*' uptake of ammonium, which was more than two times that of the perennial grasses (Yoder et al. 2000). Clearly, further study of N-uptake by perennial species with and without *Bromus* neighbors and under conditions of contrasting establishment (e.g., years with above-versus below-average precipitation) is necessary to further elucidate the mechanism of *Bromus* interference on perennial plants.

As predicted based on physiologically induced differences in phenology, declines in RGR associated with *Bromus* biomass were smaller for the evergreen shrub *Larrea* than for the grasses *Achnatherum* and *Pleuraphis*. *Larrea* is a drought-resistant perennial that maintains moderate to low rates of photosynthesis virtually all months of the year (Oechel et al. 1972; Smith et al. 1997), has high water use efficiencies through stomatal closure or increased photosynthetic capacity (Meinzer et al. 1988), and can withstand low soil water potentials (Oechel et al. 1972; Franco et al. 1994; Hamerlynck et al. 2000). In contrast, drought-evaders such as perennial grasses are sensitive to low soil water potentials, and their growing season is restricted to periods of high soil moisture (Smith et al. 1997). *Achnatherum* is an early-season C₃ species whose growth occurs above 4°C (Pearson 1979) and has lower optimal leaf temperatures for photosynthesis compared to *Pleuraphis*, a late-season C₄ grass whose growth begins in late spring (Nobel 1980). Hence, growth of *Achnatherum* is synchronous with activity of winter annuals, thereby placing *Achnatherum* in direct competition with annuals, whereas reduction in *Pleuraphis* performance by neighbors may be pronounced because of the earlier growth and rapid soil resource use of neighbors before *Pleuraphis* becomes active.

The effects of *Bromus* and mixed native annuals on perennial responses appear to be similar, based on the analyses detecting outliers from the fitted regression. Although this result is contrary to initial predictions that were based on an earlier study (DeFalco et al. 2003), the estab-

lishment of mixed species was markedly lower than *Bromus*, and thus the resulting native annual biomass was likely too low to significantly reduce perennial RGRs. Native annual species in the northern Mojave Desert germinate and grow at the same time as, but often in lower densities than, *Bromus* in any given year (Hunter 1991). Low densities of native annuals may reflect poor seedling survivorship when neighbors alter light quality (Raynal and Bazzaz 1975) or capture limited soil nutrients (Brooks 2000). However, low germination of natives in the mixed species stands in this study is consistent with the “bet-hedging” strategy found in annual species from unpredictable environments: in years with high seedling mortality, a viable portion of seed remains in the soil to germinate in subsequent years that have more favorable conditions for growth (Cohen 1966; Brown and Venable 1986; Philippi 1993; Clausen and Venable 2000). In contrast, *Bromus* has virtually no dormancy compared with native Mojave Desert annual species (DeFalco et al. 2003) resulting in the high densities and crowding effect observed for stands of *Bromus* established beneath perennials. Natives may also have lower seedling survivorship than *Bromus*, whose less exacting soil moisture and temperature requirements and greater seed viability yields greater abundance than natives (Beatley 1966). In this study, the range of densities and resulting low biomasses for the mixed species neighbors falls within the range reported for native annuals censused in the area from 1963 through 1990 (Hunter 1991). Hence, the similar perennial responses between mixed annual and *Bromus* treatments reflect the same effect of these neighbors on perennials when their abundance is low. Native annuals do not often reach the high biomass achieved by their *Bromus* counterparts; thus, negative effects of native annuals on perennials are likely infrequent.

While most research has focused on *Bromus*' dramatic impact on plant community composition and structure by providing fuel for wildfire, this study highlights the potential for the decline of perennial species in undisturbed habitat through direct interaction with *Bromus*. As *Bromus* continues to integrate into the native flora and to

dominate the landscape in the Mojave Desert, the composition of species within these communities, especially the shorter-lived perennial grasses, are subject to change even in the absence of wildfire. Future mitigation of the effects of *Bromus* in the Mojave Desert will require an understanding of the environmental cues that drive its establishment and dominance while simultaneously appreciating the interannual variation controlling these factors.

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