Sonoran Desert Winter Annuals Affected by Density of Red Brome and Soil Nitrogen

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Abstract.—Red brome [*Bromus madritensis* subsp. *rubens* (L.) Husn.] is a Mediterranean winter annual grass that has invaded Southwestern USA deserts. This study evaluated interactions among 13 Sonoran Desert annual species at four densities of red brome from 0 to the equivalent of 1200 plants m^{-2}. We examined these interactions at low (3 μg) and high (537 μg NO_3^- g soil^{-1}) nitrogen (N) to evaluate the relative effects of soil N level on survival and growth of native annuals and red brome. Red brome did not affect emergence or survival of native annuals, but significantly reduced growth of natives, raising concerns about effects of this exotic grass on the fecundity of these species. Differences in growth of red brome and of the three dominant non nitrogen-fixing native annuals at the two levels of soil N were similar. Total species biomass of red brome was reduced by 83% at low, compared to high, N levels, whereas that of the three native species was reduced by from 42 to 95%. Mean individual biomass of red brome was reduced by 87% at low, compared to high, N levels, whereas that of the three native species was reduced by from 72 to 89%.

INTRODUCTION

Winter annual species comprise 30 to 40% of Sonoran Desert floras (Rondeau *et al.*, 1996; Venable and Pake, 1999). These species contribute most of community primary production during the winter (Patten, 1978) and produce the spring wildflower blooms for which the region is famous. The abundance of these species varies widely among years, promoting the coexistence of populations through temporal partitioning of the environment (Pake and Venable, 1995). Populations of these short-lived species rely on persistent soil seeds banks for survival in these variable climates (Pake and Venable, 1996; Clauss and Venable, 2000), where they respond quickly to precipitation events and experience wide fluctuations in variable desert climates. These fluctuations may make desert annuals particularly sensitive to exotic invasive species and especially vulnerable to extirpation (Rondeau *et al.*, 1996, 2000; Venable and Pake, 1999).

Red brome (*Bromus madritensis* subsp. *rubens*) is one of a suite of winter annual grasses from the Mediterranean region that have invaded the western U.S.A. This exotic grass can reach high density and biomass, even in relatively undisturbed areas of the Sonoran (Burgess *et al.*, 1991), Mojave (Beatley, 1966; Hunter, 1991) and Great Basin Deserts (Tausch *et al.*, 1994). During years of above-average winter rain, this grass can reach densities of over 6000 plants m^{-2} (Bowers, 1987) and dominate annual communities in the Sonoran (P. Anning, pers. comm.) and Mojave Deserts (Brooks, 1998). Density and biomass of native annuals in the Mojave Desert are significantly greater when red brome is removed, suggesting that this exotic species may reduce growth of natives (Brooks, 2000). This has raised

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fears that this exotic grass may reduce survival and productivity of native annuals (Beatley, 1969; Burgess *et al.*, 1991; Hunter, 1991; Tausch *et al.*, 1994).

Temporarily immobilizing soil nitrogen (N) by applying carbon (C) sources has increased survival and growth of native perennial species, relative to exotic grasses, in western North America (McLendon and Redente, 1992; Wilson and Gerry, 1995; Young *et al.*, 1997). This response has been attributed to higher growth rates and N requirements of exotic annuals (McLendon and Redente, 1991, 1992). Native southwestern desert species evolved in low fertility soils, are expected to have low maximum potential growth rates (Chapin *et al.*, 1986) and show low responses to N addition (Williams and Bell, 1981). This is in contrast to annual *Bromus* species, which have high relative growth rates (Muller and Garnier, 1990) and show high responses to N addition (Gulmon, 1979). Red brome has shown greater response to N than Mojave Desert annuals (Hunter, 1991; Brooks, 1998, 2003), suggesting the possibility of immobilizing soil N to increase survival and growth of native Sonoran Desert annuals relative to this exotic grass.

This study used a sown community of native Sonoran Desert winter annuals, growing in containers, to characterize interactions among red brome neighbors and native annual target plants. We examined these interactions at low and high soil N to evaluate the effectiveness of immobilizing soil N for increasing survival and growth of native annuals at the population and individual levels. At the population level, we predicted that increasing densities of red brome would reduce emergence, survival, biomass and success at reaching reproductive status of native annual populations. At the individual level we predicted that increasing densities of red brome would reduce individual biomass. At each level we asked whether these effects differed between high and low levels of soil N.

MATERIALS AND METHODS

TREATMENT DESIGN

Plants grew in 33.7 × 28.6 cm rectangular plastic containers. We collected soil from a grassland area at the University of Arizona's (USA) Oracle Agricultural Center (32.4°N, 110.5°W), sieved it through a 0.6-cm mesh screen and mixed it 2:1:1 by volume; soil:mortar sand: perlite. This produced a sandy loam mix (75% sand, 15% silt and 10% clay), which was determined using a modification of the hydrometer method (Gee and Bauder, 1986).

We prepared a seed mix of 13 native Sonoran Desert winter annuals based on field abundance data (Pake and Venable, 1995; P. Anning, pers. comm.; Clauss and Venable, 2000) (Table 1). Only generic names are used in this text. Seeds of *Lupinus*, *Plantago* and *Vulpia* were obtained commercially, whereas the others were collected in the Sonoran Desert. Twenty unseeded taxa also emerged (Table 2).

Seeding densities for *Lupinus*, *Pectocarya*, *Plantago* and *Vulpia* were based on emergence from a previous study. We based densities of other species on a preliminary germination study. Seeds germinated for 21 d on moist filter paper in petri dishes sealed with electrical tape. Wide spectrum florescent lamps provided a 10.5 h photoperiod with temperatures of 20 C day/12 C night.

We estimated number of seeds sown from 100 seed weights (Table 1). The hundred seed weight of red brome was 220 mg. Seeds of *Cryptantha* were difficult to remove from fruits, so crumbled fruiting structures were sown. *Lupinus* seed was scarified immediately before sowing by boiling in water for 3 min. An estimated 1920 native annual seeds were sown per container, equivalent to 19,900 seeds m^{-2} and similar to the seed density of annual species in soil for the Sonoran Desert (Guo *et al.*, 1999).

TABLE 1.—Native Sonoran Desert annual species sown with red brome at low and high soil N, germination in Petri dishes, hundred seed weight (HSW) and seeds sown per container

Species	Family	Germ. (%)	HSW (mg)	Seeds (Num.)
Amsinckia menziesii (Lehm.) Nelson & J.F. Macbr. var. *intermedia* (Fischer & C Meyer) Gander	Boraginaceae	5	240	80
Bowlesia incana Ruiz Lopez & Pavon	Apiaceae	1	100	180
Cryptantha micrantha (Torrey) I.M. Johnston	Boraginaceae	5	n.a.¶	n.a
Descurainia pinnata (Walter) Britton	Brassicaceae	75	10	11
Eriastrum diffusum (A. Gray) H. Mason	Polemoniaceae	6	20	77
Lasthenia chrysostoma Lindley	Asteraceae	13	30	180
Lesquerella tenella Nelson	Brassiceae	1	100	180
Lupinus sparsiflorus Benth.	Fabacea	36	450	45
Parietaria hespera B.D. Hinton	Urticaceae	5	55	180
Pectocarya recurvata Johnst.	Boraginaceae	68	100	70
Plantago ovata Forsskal	Plantaginaceae	92	180	10
Stylocline micropoides A. Gray	Asteraceae	5	15	131
Vulpia microstachys (Nutt.) Munro	Poaceae	93	100	10

¶ Not available

This full-factorial study included four densities of red brome and two levels of soil N with three replications for a total of 24 containers. Seeding densities of red brome variety 'Panoche' (Pacific Coast Seed, Livermore, California, USA) ranged from 0 to 180 seeds container^{-1} (0, 45, 90 and 180 seeds container^{-1}). Nitrogen was added to high-N treatments

TABLE 2.—Species not sown, but present with native Sonoran Desert annual species and red brome at low and high soil N

Species	Family
Amaranthus sp.	Amaranthaceae
Astragalus sp.	Fabaceae
Bothriochloa ischaemum (L.) Keng	Poaceae
Bromus arizonicus (Shear) Stebb	Poaceae
Bromus carinatus Hook. & Arn.	Poaceae
Bromus hordeaceus L. ssp. *molliformis* (Godron) Maire	Poaceae
Bromus tectorum L.	Poaceae
Bromus trinii Desv.	Poaceae
Castilleja exserta (A.A. Heller) Chuang & Heckard	Scrophulariaceae
Filago californica Nutt.	Asteraceae
Muhlenbergia microsperma (DC.) Trin.	Poaceae
Lepidium lasiocarpum Torrey & Gray var. *lasiocarpum*	Brassicaceae
Opuntia sp.	Cactaceae
Schismus barbatus (L.) Thell.	Poaceae
Schismus sp.	Poaceae
Sonchus sp.	Asteraceae
Vulpia myuros (L.) C. Gmelin	Poaceae
Vulpia octoflora (Walter) Rydb.	Poaceae
Unidentified Asteraceae	Asteraceae
Unidentified Boraginaceae	Boraginaceae

as ammonium nitrate (NH_4NO_3) at the equivalent of 50 kg N ha^{-1} and sucrose ($C_{12}H_{22}O_{11}$) was added to low-N treatments at the equivalent of 550 kg sucrose ha^{-1} to stimulate growth of soil microbes and immobilize N. We sampled the surface 3 cm of soil in each container at the start of the study and again after harvest. Samples from all replications were bulked, air dried at 25 C for 3 d, then frozen until analyzed. Nitrate (NO_3^-) was determined on a water extract using an ion chromatograph (APHA, 1985).

Plants grew in a Conviron Model PGW36 growth chamber (Winnipeg, Manitoba, Canada) with cool white florescent and incandescent lamps. The photosynthetic photon flux density at 10 cm from the lamps averaged 600 ± 50 µmol m^{-2} s^{-1}. Containers were rerandomized every 14 d and watered as needed until senescence of the plants; water was not limiting in this study. The photoperiod at the start of the study was 10.3 h. To simulate winter in the Sonoran Desert, this was shortened by 5 min every 6 d to 10.0 h, then increased at the same rate to 11.7 h after 4 mo. Temperatures at the start of the study were 21.3 C day/7.2 C night. To simulate winter, the daytime temperature was decreased by 1.9 C every 12 d to 17.5 C, where it remained for 48 d, after which it increased by 1.9 C every 12 d to 25.1 C after 4 mo. The nighttime temperature was 7.2 C for the first 48 d, the lower limit of the growth chamber, then increased by 0.6 C every 12 d to 11.0 C. After 4 mo, conditions remained constant while seeds matured and plants senesced.

DATA COLLECTION

We marked each newly emerged seedling by inserting a colored toothpick into the soil next to it for 21 d at 3-d intervals. Five days after being marked, we tentatively identified seedlings and mapped locations using a Plexiglas mapping table. Data sheets were a single thickness of nearly transparent 84 cm × 102 cm, 15 mil plastic bags, which were cut along one length and opened. We identified plants to species, and noted survival two additional times, at 14 and 28 d after marking emergence.

The first cohort was the largest of the eight and included 2091 seedlings. The eighth cohort was the smallest and included 34 seedlings. A total of 4432 individuals emerged. Plants that emerged after 21 d were considered to be cohort nine, which included 220 individuals. As the mapping table could no longer be placed over the containers without damaging the plants, these were mapped based on their relationships to previously mapped plants. For survival analysis, cohort nine was considered to have emerged midway between cohort eight and the date harvest began. Plants that died after the last survival count were considered to have died midway between the last count and the start of harvest.

We harvested fruiting structures as they matured to prevent losses from shattering. Individuals of species other than *Lesquerella* were considered to have reproduced successfully if they produced at least one normal-appearing seed. As hand pollination of *Lesquerella* was not successful, individuals of this species were considered to have reproduced successfully if they produced at least one normal-appearing fruit.

After 6 mo we harvested plant shoots and major roots after loosening the surrounding soil with a 60-penny nail (a spike) and hammer. Plants dried in paper envelopes at 70 C for 2 d and total (shoot + reproductive structures + roots) biomass was determined.

DATA ANALYSES

This study used a completely randomized design with three replications of eight treatment combinations. Data from 23 of 24 containers were analyzed, due to a seeding error in one of the units. The main effects of red brome density, soil N level and species identity were considered to be fixed effects, as all were included at repeatable and nonrandom levels (Newman *et al.*, 1997).

We used the General Linear Models procedure (Proc GLM) in SAS v. 8 (SAS Institute, Inc., 1999) and Type III sums of squares for all analyses of covariance (ANCOVA) and analyses of variance (ANOVA) for these unbalanced data (Goldberg and Schneiner, 1993). Linear means are reported with standard deviations when descriptive statistics were performed on red brome data, as this grass constituted a treatment, and least squares means and standard errors are reported when inferential analyses were performed on response species data.

All data were evaluated for homoscedasticity and transformed as required. We used the Brown-Forsythe test, which compares observations to their group median (Olejnik and Algina, 1987) in JMP v. 4 (SAS Institute, Inc., 2000). This test is appropriate for completely randomized designs, where it has stable Type I error rates if data are nonnormal and when sample sizes are small or unequal (Conover *et al.*, 1981). All data also were evaluated for normality before analysis. We visually examined normal quartile plots in JMP v. 4. When selecting between a transformation that reduced heteroscedasticity and one that increased normality, we selected the former, as ANOVA is quite robust to nonnormality (Glass *et al.*, 1972).

POPULATION PARAMETERS

When evaluating emergence, survival, biomass and success at reaching reproductive status, we first performed a global ANCOVA of the interactions of the main effects with species identity (Goldberg and Scheiner, 1993). Significant global interactions indicated that differences among species varied with main effects, after which we performed ANOVA by species. When species means were separated in global analyses, we used the Tukey-Kramer adjustment for multiple comparisons in Proc GLM, SAS v. 8. To answer specific questions about significant effects on species, we used single-degree-of-freedom contrasts.

We analyzed the effects of red brome density and soil N level on percent emergence of the ten sown species that emerged in at least one replication of each treatment combination using arcsin square root [arcsin$(\sqrt{x})$] transformed percent data. We analyzed mortality of individuals that died before being positively identified on log-transformed count data.

The 11 dominant species were included in analysis of survival. These included the ten sown species that emerged in at least one replication of each treatment combination, plus unseeded *Bothriochloa*. We performed a global analysis using the Proportional Hazards Regression procedure (Proc PHREG) in SAS v. 8. This semiparametric procedure uses the Cox regression method (Cox, 1972), which combines a proportional hazards model and a maximum partial likelihood estimation (Allison, 1995).

We analyzed the effects of red brome density and soil N on total species biomass of the same 11 species using square root [$\sqrt{(x \neq 1)}$] transformed data. Untransformed counts were used to analyze success at reaching reproductive status of emerged individuals of nine of the 11 dominants; *Bothriochlora* did not reproduce in this study and reproduction of *Parietaria* was rare enough to preclude analysis.

INDIVIDUAL BIOMASS

We analyzed the effects of red brome density and soil N level on mean individual biomass (shoot + root) of the 11 dominant species using arcsin square root transformed biomass data.

RESULTS

Red brome treatment densities ranged from the equivalents of 292 to 1168 plants m^{-2} (Table 3). Although density increased approximately four-fold from low to high density, biomass increased by only 25%, due to a concomitant 70% decrease in the mean individual

TABLE 3.—Red brome density and biomass when growing with Sonoran Desert annual species at three densities (low, medium, high) and two soil N level (low, high)

	Red brome density		
	Low	Medium	High
Density (plants m^{-2} ± SD)	292 ± 63	607 ± 101	1168 ± 189
Species biomass (g ± SD)	9.83 ± 9.1	11.5 ± 9.2	12.33 ± 9.9
Individual biomass at low N (mg ± SD)	55.5 ± 24	48.7 ± 14	28.2 ± 2.0
Individual biomass at high N (mg ± SD)	776 ± 355	361 ± 47	202 ± 62

size of red brome. These densities were well within the range reported for red brome in the western USA, which can reach 6780 plants m^{-2} (Bowers, 1987).

Initial soil NO_3^- levels in low- and high-N treatments averaged 2.87 ± 0.6 SD and 537 ± 90 SD µg NO_3^- g soil^{-1}, respectively. High-N treatments were within the range reported for agricultural soils near Tucson, Arizona, which range to over 800 µg NO_3^- g soil^{-1} (Warrick *et al.*, 1992). After harvest, low- and high-N treatments averaged 4.44 ± 0.71 SD and 6.61 ± 1.5 SD µg NO_3^- g soil^{-1}, respectively.

SPECIES IDENTIFIED

Thirty-two taxa, including red brome, were found in this study (Tables 1, 2). Twenty-five were identified to species and seven (16 individuals) were identified to genus or family. These taxa accounted for 80% of emerged individuals and 100% of final biomass. The other 20% of emerged individuals did not survive 28 d and were only tentatively identified.

Eleven of the 13 native annual species sown emerged and survived; *Bowlesia* and *Cryptantha* did not. *Descurainia* was represented by five individuals and was not included in population analyses. Data for the eight most numerous species showing the greatest number of significant differences among treatments combinations are presented in figures. Twenty unseeded taxa were also present (Table 2). Five species of *Bromus* occurred only in red brome treatments, suggesting that they were added in seed. Unseeded taxa included an exotic *Bothriochloa* sp., most likely *B. ischaemum* (L.) Keng. Although a warm season (C_4) perennial, this grass apparently was able to persist due to the relatively high (7.2 C) minimum temperature, the lowest possible in the growth chamber.

POPULATION PARAMETERS

Emergence.—An interaction of species with N (P < 0.0001) indicated that differences in emergence of native species varied with soil N level, but the lack of an interaction of species with red brome (P = 0.99) indicated that these differences did not vary with red brome density. Emergence of *Lupinus* and *Plantago* was higher (P < 0.01) in low-N treatments, whereas that of most other Sonoran Desert species higher in high-N treatments (Fig. 1). Red brome emergence was higher in low-N treatments (Table 4). Emergence of all wild-collected seed was <6% of sown seeds. Species differed in their relative times of emergence. *Plantago* had the earliest emergence, with 95.1% of individuals in the first two cohorts, or first 6 d. Red brome was among the earliest three species to emerge, with 86.8% of individuals emerging in the first 6 d.

Survival.—More individuals per container (P < 0.0001) survived fewer than 5 d in high-N (mean 25.0 ± 1.8 SE) than in low-N (mean 8.84 ± 1.7 SE) treatments. However, overall survival of the 11 dominant species was higher (P = 0.02) in high-N (51.9%) than in low-N treatments (38.7%). There was no significant effect of red brome density on either survival
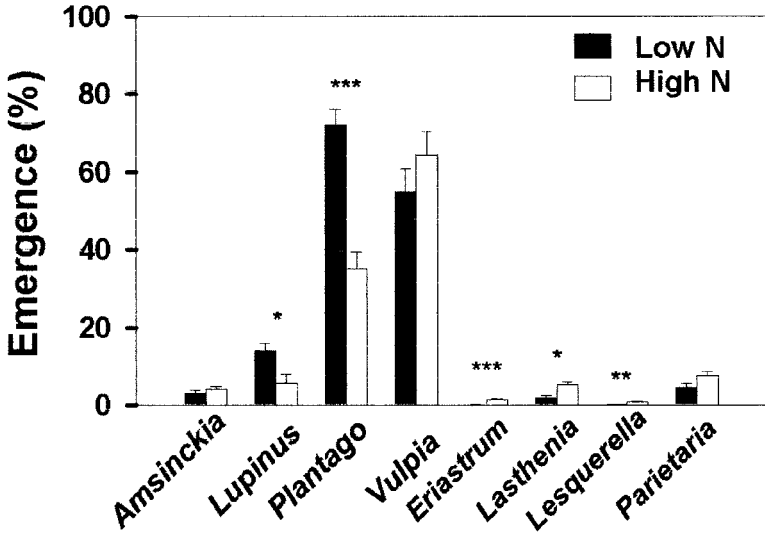
FIG. 1.—Emergence (percent + 1 SE) of Sonoran Desert annual species growing with red brome at low and high N levels. Differences between treatments significant at *P*: * < 0.01, ** < 0.001, *** < 0.0001

to 5 d (P = 0.15) or overall survival of the 11 species (P = 0.19). The lack of any significant interaction of species with main effects (P ≥ 0.05) indicated that species did not differ in their responses to treatments. Overall survival varied widely among species, ranging from ≥80% of emerged individuals of *Lupinus*, *Plantago* and *Vulpia*, to <15% of *Parietaria* and *Pectocarya*. Survival of red brome was similar in the two N treatments (Table 4).

Species biomass.—Interactions of both species with red brome (P < 0.0001) and species with N (P < 0.0001) indicated that differences in species biomass varied with both main effects. Total biomass of *Lupinus* was greater (P < 0.0001) in low-N treatments, whereas biomass of all presented species other than *Plantago* was greater (P ≤ 0.01) with high N (Fig. 2). Total biomass of red brome, averaged over all densities, was greater in high-N than in low-N treatments (Table 4).

Red brome density affected (P < 0.05) total biomass of *Amsinckia*, *Lasthenia*, *Parietaria*, *Plantago* and *Vulpia* (Fig. 2). Single-degree-of-freedom contrasts revealed that species

TABLE 4.—Red brome emergence, survival, success at reaching reproductive status and biomass when growing with Sonoran Desert annual species at two soil N level (low, high)

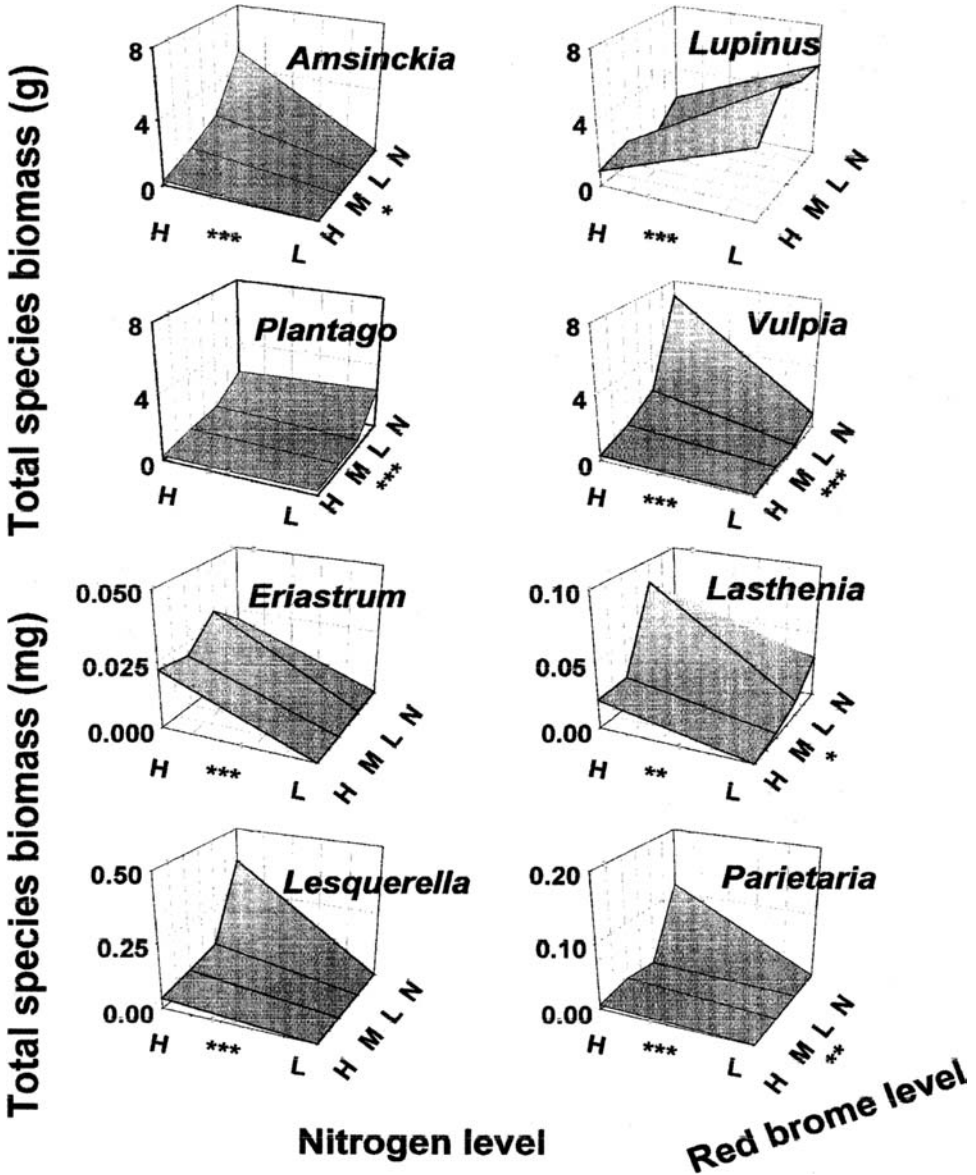|	N level	
	Low	High
Emergence (% ± SD)	76.5 ± 5.7	57.7 ± 7.1
Survival (% ± SD)	93.9 ± 4.7	94.1 ± 5.1
Success at reproductive status (% ± SD)	94.5 ± 3.9	94.5 ± 4.9
Species biomass (g ± SD)	3.0 ± 1	19.5 ± 3.9
Individual biomass (mg ± SD)	44 ± 20	446 ± 32

Fig. 2.—Total species biomass per container of Sonoran Desert annual species growing with four densities of red brome [high (H), medium (M), low (L), and none (N)] and at low (L) and high (H) N levels. Differences between treatments significant at *P.* * < 0.01, ** < 0.001, *** < 0.0001

biomass was greater (P < 0.05) without red brome, indicating interference of this exotic grass with these Sonoran Desert species. *Lupinus* produced similar species biomass growing with red brome and without and did not exhibit a net competitive response (sensu Goldberg, 1990) to red brome neighbors.
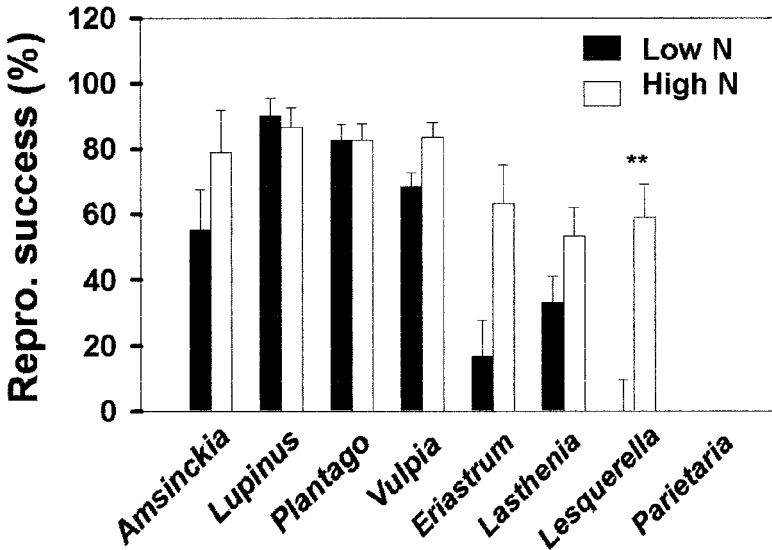
Fig. 3.—Success at reaching reproductive status (percent + 1 SE) of Sonoran Desert annual species growing with red brome at low and high N levels. Differences between treatments significant at P: ** < 0.001

Three species, *Amsinckia, Plantago* and *Vulpia*, were affected (P < 0.01) by interactions of N with red brome. Species biomass of each was reduced by a greater percentage when growing with red brome in high-N treatments than in low. Reductions in total species biomass in low N, compared with high N, were similar for red brome and the three dominant non-N fixing native annuals in this. At the medium density of red brome, these ranged from a reduction in species biomass of 42% for *Plantago* to 95% for *Vulpia*, compared with 83% for red brome. Declines in species biomass of each of the 11 analyzed species growing with red brome, over both N levels, averaged 58.4% of biomass produced when this grass was not present.

Reproductive status.—Interactions of both species with red brome (P < 0.02) and species with N (P < 0.0001) indicated that differences in success at reaching reproductive status of the nine analyzed species varied with both main effects. Success at reaching reproductive status of *Eriastrum, Lesquerella* and *Vulpia* was higher (P < 0.03) in high-N than in low-N treatments (Fig. 3) and no species had significantly higher success at reaching reproductive status in low-N than in high-N treatments. Success of red brome was similar at both N levels (Table 4). Analysis by species failed to reveal a significant effect (P < 0.05) of red brome on success at reaching reproductive status of any species.

Individual biomass.—Interactions of both species with red brome (P < 0.05) and species with N (P < 0.0001) indicated that differences in individual biomass varied with both main effects. Individuals of *Lupinus* were larger (P < 0.0001) in low-N treatments, whereas individuals of all species presented, other than *Amsinckia*, were larger (P < 0.002) in high-N treatments (Fig. 4). Red brome individuals, averaged over all densities, were larger in high-N than in low-N treatments (Table 3). Red brome density affected (P ≤ 0.002) biomass of individuals of *Lasthenia, Plantago* and *Vulpia* (Fig. 4). *Lupinus* produced similar-sized individuals growing with red brome and without, again showing no net competitive response to red brome neighbors.
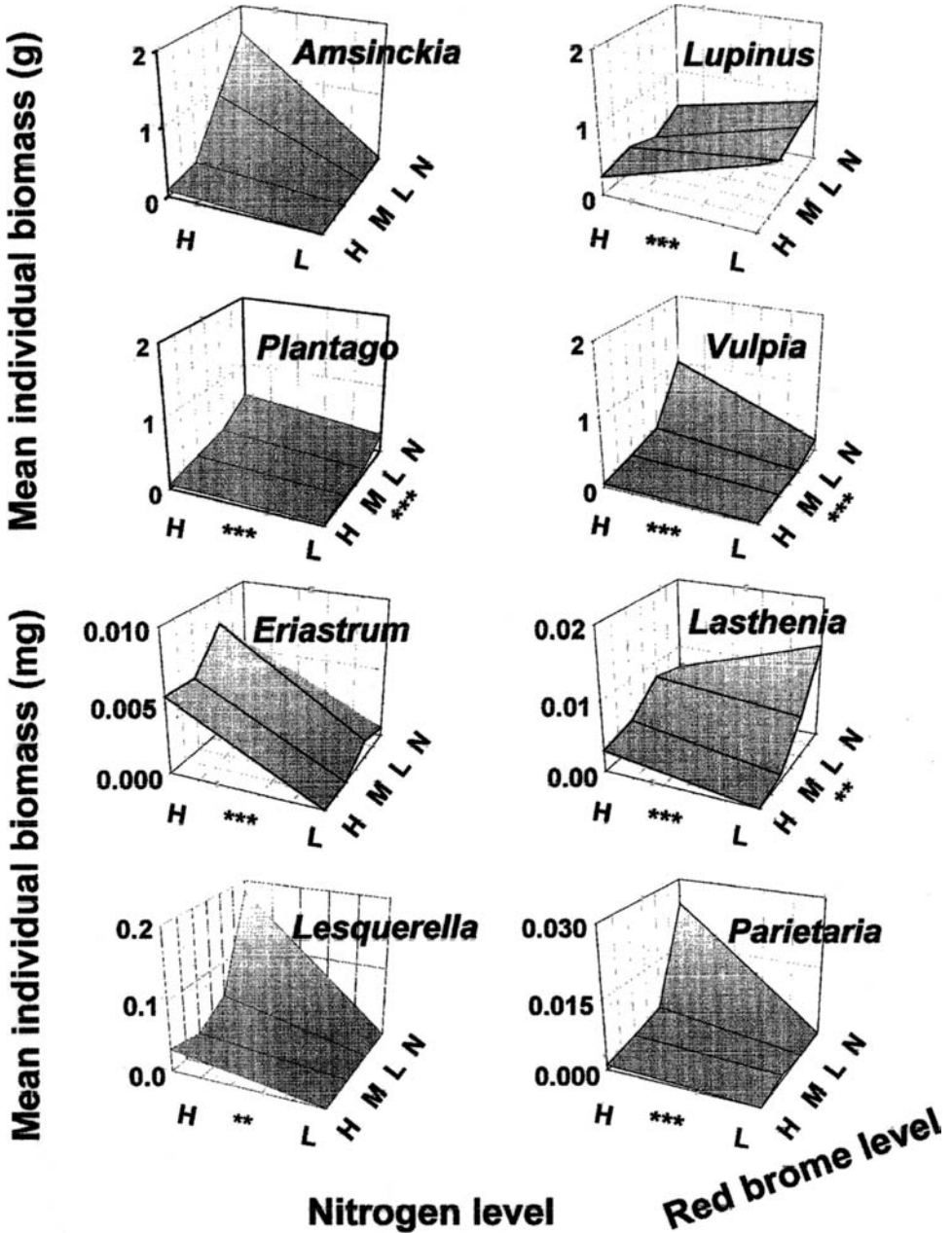
FIG. 4.—Individual biomass of Sonoran Desert annual species growing with four densities of red brome [high (H), medium (M), low (L), and none (N)] and at low (L) and high (H) N levels. Differences between treatments significant at *P*: ** < 0.001, *** < 0.0001

Two species were affected (P $\leq$ 0.002) by interactions of N with red brome. Effects on individual biomass of *Vulpia* were similar in direction and magnitude to those for species biomass. However, individual biomass of *Lasthenia* was reduced to a far greater extent by the presence of red brome in low-N treatments (83%) than in high-N (25%). The size of red brome individuals was reduced more (74%) when conspecific density quadrupled in high-N than in low-N (50%) treatments (Table 3). Reductions in mean individual biomass in low N, compared with high N, were similar for red brome and the three dominant non-N fixing native annuals in this study. At the medium density of red brome, these ranged from a reduction in individual biomass of 72% for *Amsinckia* to 89% for *Vulpia*, compared with 87% for red brome.

<div align="center">DISCUSSION</div>

<div align="center">RED BROME EFFECTS</div>

Red brome did not affect emergence or survival of native Sonoran Desert annuals in this study and had little effect on their success at reaching reproductive status. However, this exotic grass significantly reduced growth of most native species. This raises concerns over the long-term survival of these populations, due to the direct relationship between individual size and fecundity of winter annuals (Mack and Harper, 1977; Gulmon, 1979; Inouye *et al.*, 1980).

Emergence and survival were relatively insensitive to increasing red brome density. Other studies also have found little effect of density on survival of Sonoran (Inouye *et al.*, 1980) or Negev Desert (Kadmon and Shmida, 1990) annuals when water is adequate. The phenotypic plasticity of Southwestern desert annuals allows them to survive and to reproduce, although as very small individuals producing only a few seeds, when resources are limiting (Tevis, 1958; Went, 1949). The reduced size of native annuals growing with red brome raises concern for the future of these species, which depend on soil seed reserves for their continued existence (Pake and Venable, 1996).

Species biomass of native annuals was significantly lower when growing with red brome, and *Lasthenia* and *Vulpia* were also sensitive to the density of red brome neighbors. Only *Lupinus* seemed relatively insensitive to the presence or density of red brome. Other studies have also found growth to be the aspect of performance of Sonoran (Inouye *et al.*, 1980) and Negev Desert (Kadmon and Shmida, 1990) winter annuals most affected by increasing density.

As water was not limiting in this study, increasing density of red brome likely reduced growth of native species through interference for light or for N. It seems unlikely that interference for light occurred in low N treatments, due to the small size of individuals in these treatments. It further seems unlikely that this was the mechanism that reduced growth of tall native species, such as *Amsinckia*, which was similar in height to, or taller than, red brome in this study. It appears more likely in these cases that red brome reduced growth of native species through interference for soil N, even in high-N treatments.

<div align="center">NITROGEN EFFECTS</div>

Nitrogen level affected both emergence and survival of Sonoran Desert species in this study. Differences in species' emergence likely reflected adaptation to different fertility levels. Lower emergence of *Lupinus* in high-N treatments was likely due to it being a leguminous N-fixer, whose germination is inhibited by high levels of soil NO_3^- (Quispel, 1974). *Plantago* may also be adapted to relatively low-fertility sites, as total biomass of this species did not respond to N addition in this study, or on wildland sites (Williams and Bell, 1981). Conversely, three species were nearly absent from low-N treatments and reports

suggest they may be adapted to relatively high-fertility sites. *Lepidium* and *Lesquerella* respond strongly to N addition on wildland sites (Gutierrez *et al.*, 1988; Mun and Whitford, 1989) and *Parietaria* is most abundant under canopies of perennial woody species (Hickman, 1993) where nutrient levels are relatively high (Brooks, 1999; Smith *et al.*, 2000).

Early seedling mortality was almost three times higher in high-N than in low-N treatments. Although these individuals were not identified, they may have been *Lupinus* and *Plantago*, as emergence of these species was lower in high-N treatments. In addition, browning of early leaves, consistent with N toxicity, was noted in *Lupinus* during the first 28 d. In contrast to the pattern at establishment, subsequent survival was higher with high N. Greater subsequent mortality in low-N treatments may have been due to greater numbers of very small individuals produced in these treatments.

Most Sonoran Desert species had greater species biomass at high N, with *Lupinus*, the only N-fixer, being the exception. This is in contrast to findings in a Mojave Desert field study, where exotic biomass increased, but native annual biomass decreased, with N addition (Brooks, 2003). However, that study did not separate out the effects of interactions with exotic annuals, including red brome, and attributed the reduction in growth to increased interference for water and nutrients (Brooks, 2003). Although the current study manipulated only soil N level, other unmanipulated and unanalyzed nutrients may have been involved in interactions among species in this study. Differences in growth of red brome and of native annuals at low and at high fertility were similar in magnitude, casting doubt on immobilization of soil N as a technique to enhance growth of native annuals relative to this exotic grass.

<center>LONG-TERM IMPLICATIONS</center>

Although we found clear evidence of reduced growth and possible reduced fecundity of Sonoran Desert annuals growing with red brome, our study can shed little light on the final outcome of these interactions (Gibson *et al.*, 1999). Although the prospect of lower native annual fecundity raises the possibility of declines in their seed banks, species react individually to changes in their environment and these interactions will occur in an environment with high spatial and temporal heterogeneity.

Sonoran Desert species with large seed (*Amsinckia*, *Lupinus* and *Plantago*, Table 1) and early emergence (*Amsinckia* and *Plantago*) had high survival and growth, and their growth was affected least by the presence of red brome. These traits have been linked to high survival and growth of annual species in other systems (Ross and Harper, 1972; Gulmon, 1977; Mack and Harper, 1977; Goldberg and Miller, 1990). Together, these traits allow preemption of resources early in the growing season, when this may be most critical (Ross and Harper, 1972), and when seasonal moisture provides an ephemeral increase in available soil N (Cui and Caldwell, 1997).

Populations of red brome are dramatically reduced during drought in the Sonoran (Burgess *et al.*, 1991; L. F. Salo, pers. obs.) and Mojave Deserts (Hunter, 1991; Brooks, 1999). Native species are able to recover from persistent soil seed banks (Pake and Venable, 1995; Clauss and Venable, 2000) when precipitation returns to normal levels (Hunter, 1991), but red brome populations depend on dispersal of seed produced in the few favorable microsites available during drought (Brooks, 1999). Rather than relying on seed dormancy, red brome relies on seed dispersal, hedging its bets in space, rather than time (Salo, 2004). These periods of adequate moisture after drought, when red brome densities are low, provide the greatest opportunity for native southwestern USA winter annuals to replenish their seed banks (Salo, 2004). Although fears that red brome may reduce seed banks of native annual

species (Hunter, 1990; Brooks, 2000) are well founded, these effects will likely be dampened by the wide fluctuations in density and biomass that characterize this exotic grass.

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