ARE MOJAVE DESERT ANNUAL SPECIES EQUAL? RESOURCE ACQUISITION AND ALLOCATION FOR THE INVASIVE GRASS *BROMUS MADRITENSIS* SUBSP. *RUBENS* (POACEAE) AND TWO NATIVE SPECIES[1]

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Abundance of invasive plants is often attributed to their ability ot outcompete native species. We compared resource acquisition and allocation of the invasive annual grass *Bromus madritensis* subsp. *rubens* with that of two native Mojave Desert annuals, *Vulpia octoflora* and *Descurainia pinnata*, in a glasshouse experiment. Each species was grown in monoculture at two densities and two levels of N availability to compare how these annuals capture resources and to understand their relative sensitivities to environmental change. During >4 mo of growth, *Bromus* used water more rapidly and had greater biomass and N content than the natives, partly because of its greater root-surface area and its exploitation of deep soils. *Bromus* also had greater N uptake, net assimilation and transpiration rates, and canopy area than *Vulpia*. Resource use by *Bromus* was less sensitive to changes in N availability or density than were the natives. The two native species in this study produced numerous small seeds that tended to remain dormant, thus ensuring escape of offspring from unfavorable germination conditions; *Bromus* produced fewer but larger seeds that readily germinated. Collectively, these traits give *Bromus* the potential to rapidly establish in diverse habitats of the Mojave Desert, thereby gaining an advantage over coexisting native species.

Key words: *Bromus madritensis* subsp. *rubens*; desert ephemerals; introduced annual grasses; Mojave Desert; nitrogen uptake; plant biomass; Poaceae; root system; seed production; *Vulpia octoflora*; water uptake.

Annual grasses and forbs introduced from the Mediterranean have invaded plant communities in arid regions of North America (Billings, 1990; D'Antonio and Vitousek, 1992). Abundant attention has focused on introduced plants in the intermountain West (Hulbert, 1955; Harris, 1967; Billings, 1990), California grasslands (Gulmon, 1979; Gordon et al., 1989; Huenneke et al., 1990; Gordon and Rice, 1993; Holmes and Rice, 1996), and coastal sage scrub of southern California (Eliason and Allen, 1997). A high abundance of invasive annuals has also been documented in the warm deserts of North America (Beatley, 1966; Brown and Minnich, 1986; Brooks, 1999).

The annual grass *Bromus madritensis* subsp. *rubens* was introduced into western North America more than a century ago with other species of the genus *Bromus* (Hulbert, 1955). Density and biomass of *B. madritensis* in the Mojave Desert appears to have been initially low early in the 20th century, but abundance increased sharply in the 1970s, and *B. madritensis* is now dominant across many landscapes in the warm deserts of North America including the Mojave Desert (Beatley, 1966; Brooks, 1999; Hunter, 1991). The establishment and spread of *B. madritensis* may be similar to that of its congener *B. tectorum*, whose success in the intermountain West has been facilitated by competitive displacement of native perennial species (Harris, 1967). *Bromus tectorum* is particularly competitive after wildfire because its rapid root growth quickly depletes soil resources, leaving little water and nutrients available for other species (Melgoza et al., 1990; Melgoza and Nowak, 1991).

Studies of annual plant populations in the Mojave Desert have generated contrasting conclusions on the competitive interactions between native annual species and *Bromus madritensis* subsp. *rubens* (hereafter referred to as *Bromus*). Initially, *Bromus* was described as "not aggressive" (Beatley, 1966), and increases in the abundance of *Bromus* were not correlated with marked decreases in native annual species (Beatley, 1966; Hunter, 1991). Because coexisting species may reduce competition by partitioning resources through differences in rooting patterns (Gulmon et al., 1983; Gordon and Rice, 1992), differences in root morphology (fibrous roots of *Bromus* vs. taproots of most native annuals) were speculated to allow coexistence between *Bromus* and native annuals (Hunter, 1991). Additionally, variability in soil N levels in deserts allows for species with different N requirements to coexist (Gulmon, 1979; Williams and Bell, 1981; Gutierrez and Whitford, 1987). In contrast, recent studies suggest that *Bromus* and native annual species may compete. For example, the addition of N fertilizers beneath *Larrea tridentata* canopies increased *Bromus* biomass and decreased native annual plant biomass in a year with high precipitation (Brooks, 2003). Furthermore, removal of *Bromus* individuals from mixed annual plant com-

munities increased the density and shoot biomass of native annual species in the Mojave Desert of California (Brooks, 2000). Unfortunately, no studies have examined the mechanisms by which this *Bromus* species may outcompete coexisting native Mojave Desert species or determined unequivocally that *B. madritensis* subsp. *rubens* has a greater competitive potential than ecologically similar native winter annuals.

The main goals of this study were: (1) comparing resource acquisition by the invasive annual grass *B. madritensis* subsp. *rubens* and two native Mojave Desert annuals, with particular focus on density and N effects; and (2) comparing resource allocation between vegetative growth and reproduction for these species. Each species was grown in monoculture in a glasshouse experiment to differentiate the effect of a particular species on resource availability, an important component of competition, from the responses of target species to a particular neighbor (Goldberg, 1990). Concurrent field and greenhouse studies document the responses of native Mojave Desert perennial species associated with these annual plants as neighbors. All three species were grown in soils with low and high N availability because soil nutrients vary spatially in the Mojave Desert (Titus et al., 2002). Plant density was also manipulated because annual plant densities fluctuate greatly from year to year as precipitation varies (Beatley, 1974), which could influence resource acquisition. Plant responses to these variations in soil N and plant density provide insight into the sensitivity of invasive and native species to environmental changes and heterogeneity of resource availability. We hypothesized that *Bromus* would have greater resource uptake, and hence higher biomass and tissue N content and reproductive output, than the native species. *Descurainia pinnata* and *Vulpia octoflora* were selected for this study because they represent two growth forms common to native winter annual floras (forb and grass, respectively). In addition, these species are widespread throughout the Mojave Desert, are found in similar microhabitats as *Bromus*, and thus potentially compete with *Bromus* (Went, 1949; Samson, 1986; Brooks, 2000; DeFalco et al., 2001). We also hypothesized that *Bromus* would be less sensitive to changes in N availability and plant density than the native species. To understand what may cause the differences in resource uptake and allocation, we also compared the physiological and morphological traits of *Bromus* with those of the natives.

MATERIALS AND METHODS

Soil resource use, biomass and N allocation, and reproduction were compared between *Bromus* and two native annual species grown in a glasshouse at the University of Nevada, Reno, Nevada, USA. Thirty-six 170-L plastic barrels were arranged in a random complete block design to control for potential variability in light and temperature within the glasshouse. The three species, two plant densities, and two N levels were randomly assigned to 12 barrels within each of three replicate blocks. Barrels were filled with washed river sand and watered one time with a modified Hoagland's solution to barrel capacity prior to planting seeds. Fertilized barrels received essential levels of micro- and macroelements plus NH_4NO_3, and nonfertilized barrels were watered with the same concentrations of essential elements but without any NH_4NO_3 (background levels of N were already low). The control and fertilized N levels at the time seeds were planted (1.4 and 11.5 µg N/g dry soil, respectively) were within the ranges reported for soils in interspaces and beneath shrub canopies in the Mojave Desert (Nishita and Haug, 1973; Rundel and Gibson, 1996).

Seeds of *Bromus madritensis* subsp. *rubens* (L.) Husnot (Poaceae), *Descurainia pinnata* (Walter) Britton (Brassicaceae), and *Vulpia octoflora* (Walter) Rydb. (Poaceae) were collected from multiple individuals in the northeast Mojave Desert and pooled by species before planting. Based on germination tests for each species, seeds were over-sown in the barrels to obtain target densities of 80 and 800 individuals/m². Seeds were misted with tap water until seedlings were established (approximately 2 wk) and then soils were allowed to dry at the extant evapotranspiration rate. Seedlings were thinned after 4 wk to obtain target densities. The average plant density for the high-density treatment (mean ± SE, 792 ± 14 seedlings/m²) was very close to our target density, but the low-density treatment (133 ± 18 seedlings/m²) was greater than our target because seeds germinated immediately after thinning. Nonetheless, density was not significantly different among species or between N fertilization levels at this stage ($P = 0.56$ and 0.64, respectively). These densities are within the range of natural densities of mixed species stands (*Bromus* + natives) in years of low and high productivity for annual plants in the northeast Mojave Desert (Hunter, 1991).

Stand-level water use—Stand-level water use for *Bromus* and the native species was determined by weighing barrels weekly using a scale (Challenger Model 3260, Measurement System International, Seattle, Washington, USA) suspended from a mobile steel frame. The relationship between the volume of water lost (y) and time (x) was described for each barrel using the sigmoidal equation $y = a/(1 + \exp(-(x - x_0)/b))$, where a, b, and x_0 are constants ($r^2 = 0.97$–0.99, SigmaPlot 2000, version 6.10, SPSS, Chicago, Illinois, USA). Using the first derivative of this equation, we plotted the instantaneous rate of stand-level water use for each date, integrated the area under this curve using the trapezoidal rule (milliliters per day times day), and finally divided this area by the lifespan of the stand (in days) to determine the average rate of water use (in milliliters per day). The total water use of the stand (in liters) over the duration of the experiment was determined from the loss of mass at final harvest. An aluminum tube (4.0-cm inner diameter, 4.1-cm outer diameter) was installed vertically in the center of each barrel prior to planting, and a calibrated neutron probe (Hydroprobe Moisture Depth Gauge, Campbell Pacific Nuclear, Martinez, California, USA) was used to measure soil volumetric water content (Θ_{vol}) at the 0.3-, 0.5-, and 0.7-m depths every time barrels were weighed.

Canopy leaf and root surface areas—Canopy leaf area was determined approximately every 2 wk for the duration of the experiment by multiplying the average leaf area per individual plant by the total number of plants per barrel. Three individual plants were randomly selected in each barrel on every sampling date. For *Bromus* and *Vulpia*, canopy leaf area per individual plant was estimated by multiplying the total number of leaf blades per plant by an average area per leaf. Average area per leaf was estimated as an elongated triangle (0.5 × blade length × blade basal width above the ligule) for 3–5 leaf blades per plant. For *Descurainia*, canopy leaf area per individual plant was the sum of the areas of all leaves, which were estimated with a transparent 0.25-cm² grid. These methods for determining leaf areas were validated by comparing estimates from individuals collected at final harvest to actual area measured on a leaf area meter (Li-3000A, LI-COR, Lincoln, Nebraska, USA). Estimated canopy leaf areas (in square meters) were plotted through time (in days), and the average canopy leaf area was determined as the integrated area under this curve (in square meter days) using the trapezoidal rule and dividing by the time interval that the measurements were collected (in days).

Soil cores were extracted from the barrels to determine root surface area using a 10-cm-diameter, 6-cm-deep soil tin (471 mL) when stands began to senesce. Cores were collected from tins centered at two depths (0.3 and 0.7 m) so that roots represented the 0.25–0.35 m and 0.65–0.75 m depths. Winter annuals of warm deserts generally produce the majority of their roots within the top 0.3 m of soil (Forseth et al., 1984), but deeper soils were sampled because *Bromus* spp. are known to produce roots to a depth of 1 m (Hulbert, 1955). Roots were rinsed from soil and stained for 30 min with Congo red dye. After blotting excess moisture and dye with paper towel, roots were placed on a plastic transparency sheet and scanned on a flatbed scanner using Imaging for Windows (Wang Laboratories, Billerica, Massachusetts, USA). Root surface area was determined from the root image files processed by

GSRoot software (Louisiana State University Agricultural Station, Baton Rouge, Louisiana, USA).

Leaf and root physiology—Instantaneous gas exchange was measured for each species every 1–2 wk during the course of the experiment. Leaf-level gas exchange was measured on the most recently expanded leaf on two of the three replicate barrels per treatment combination using a programmable, open-flow gas exchange system (Li-6400, LI-COR). Leaf temperature was set at 25°C, and the cuvette reference CO_2 concentration maintained at 350 μmol/mol using a CO_2 injector. Leaf area was determined from an image of the leaf produced on photosensitive diazo paper and run through a leaf-area meter (Li-3000A, LI-COR). Net assimilation (in micromoles CO_2 per square meter per second) and transpiration (in millimoles H_2O per square meter per second) rates were plotted through time (in days), and the average rates were determined in SigmaPlot as the integrated area under each curve divided by the time interval that measurements were collected.

Uptake of $^{15}NH_4$ and $^{15}NO_3$ was performed on excised root segments (<1 mm diameter) from the upper 0.3 m of soil according to methods modified from Chapin and Van Cleve (1989). Roots of this diameter were uncommon in the low-density treatment for all species and for *Descurainia* and *Vulpia* at high density and low N. Thus, N uptake could only be measured for all three species in the high density × high growth N treatment and for *Bromus* and *Vulpia* in the high density × 1000 μmol/L ^{15}N solution treatment (see later). Soil was collected in a 3-cm-diameter, 25-cm-deep soil core, and roots were gently freed with deionized water. Roots were blotted on cheesecloth, and a 1-g sample was quickly weighed and transferred to a double-layer square of cheesecloth (10 cm on the side) with a course weave (1 × 2 mm). The edges of the cheesecloth were quickly gathered and secured with cotton string before placing the bagged root segments into aerated buffered 0.5 mmol/L $CaCl_2$ at 20°C for 20 min. Samples were then immersed in either a low (100 μmol/L) or high (1000 μmol/L) $^{15}NH_4Cl$ or $K^{15}NO_3$ solution for 30 min at 20°C and aerated. Excess ^{15}N adsorbed to the root surface after labeling was removed by briefly immersing the sample in 1 mmol/L KCl maintained at 5°C. Roots were then removed from cheesecloth bags, dried in a convection oven at 75°C for at least 48 h, and ground using a dental amalgam mill. Dried roots were weighed and sent to the University of California, Berkeley, California, USA for isotopic analysis according to Harris and Paul (1989) using an automated ^{15}N-analysis continuous-flow isotopic-ratio mass spectrometer system (Europa Scientific, Cincinnati, Ohio, USA).

Stand biomass and N content—Once stands senesced, plant tissues were harvested. Shoots were cut at the soil surface and separated into vegetative and reproductive components. The roots that were collected to determine root surface area were used to estimate total barrel root biomass and N content. All harvested tissues were dried in a convection oven at 40°C to a constant mass, weighed, and ground in a Wiley mill through a 40-mesh screen for N analysis in a Perkin-Elmer elemental analyzer (PE2000, Lincoln, Nebraska, USA). Aboveground biomass and N content were determined directly from the whole barrel harvests. Total biomass and N content of roots were extrapolated to the whole barrel by assuming uniform distribution of roots within the soil and that the average root biomass from the 0.3- and 0.7-m depths was representative of the mean root biomass.

Biomass allocation between roots, shoots, and reproduction—Mature seeds were collected as they dehisced from senescing plants or separated from inflorescences at final harvest by hand or using a seed thrasher. For each barrel, multiple replicate samples of seeds between 0.1 and 1.0 g were weighed, and the number of actual seeds was counted to make a predictive model; the remaining seeds were weighed in increments within the range of the predictive model and summed to estimate the total seed count for each barrel. Net reproductive effort per plant was estimated as the mass of seeds divided by the total vegetative biomass at final harvest (sensu Harper and Ogden, 1970). Root : shoot ratio was calculated as the estimated stand root biomass divided by the stand shoot biomass for each pot.

Seed germination and dormancy—Seed germination was determined from 50 seeds randomly selected from each barrel and split into two replicate groups (25 seeds each). Seeds were germinated in petri dishes in the dark at room temperature on #2 Whatman filter paper moistened with deionized water. Seeds were checked daily for 15 d, and germinated seeds were counted and removed; a seed was considered germinated once the radicle emerged. Seeds that did not germinate after 15 d may have been viable but were dormant. Therefore, ungerminated seeds were soaked for 12 h in deionized water, and the seed coat was either pierced with a needle (*Descurainia*) or cut longitudinally with a razor blade (*Bromus* and *Vulpia*). Seeds were soaked in a 0.1% 2,3,5-tetrazolium chloride red dye for 2–4 h (*Bromus* and *Vulpia*) or up to 8 h (*Descurainia*). The dye was removed with an eyedropper and cleared with a solution of lactic acid, phenol, and glycerol in equal volumes for 30 min. Viability was determined by examining the embryo with a dissection scope (Grabe, 1970). Percent germination was calculated based on the total number of seeds.

Statistical analysis—Initially, all response variables were run as random complete block ANOVAs; however, the block effect was never significant at $\alpha < 0.05$ for any response variable tested. Consequently, all statistics reported are for a completely randomized design. Most responses were analyzed using a three-factor ANOVA. Species, plant density, and N availability were all fixed effects. Analysis of root surface area also included soil depth as a fixed effect. The species effect determined overall differences in responses between *Bromus* and the native species. The two-way interactions (N × species and density × species) were of particular interest because they compared the sensitivities of *Bromus* and the native species to N and density effects. Single-df contrasts were constructed by partitioning the between-groups sums of squares to test specific hypotheses when these interactions were significant (Quinn and Keough, 2002). These hypotheses included comparing the difference in responses between high and low N availability (or high and low density) for *Bromus* with the difference in these responses for each native species separately. Typically, the other interactions were not significant. But when the density × N × species interaction was significant, separate two-way ANOVAS (N × species) were run at each density level. N uptake was analyzed in two separate three-factor ANOVAs (species × concentration of inorganic N solution × inorganic N form and species × growth N availability × inorganic N form). For all ANOVAs, violation of the assumption of equal variance was examined in residual plots and using Levene's test for equal variance. Violation of normality was examined in normality plots and tested according to D'Agostino (1971). Heteroscedastic data were log_{10}-transformed to meet the assumption of equal variance (Box and Cox, 1964).

RESULTS

Stand-level water use—Stands of *Bromus* used water more rapidly, which resulted in greater total water use, and were less sensitive to N availability and plant density compared with stands of native species. Mean water use rate ($\pm$SE) was greater for *Bromus* (213 $\pm$ 8 mL/d) than for either *Descurainia* (187 $\pm$ 14 mL/d) or *Vulpia* (142 $\pm$ 15 mL/d; species effect, $P < 0.01$). These rapid rates resulted in greater total water use ($P < 0.01$) and lower final Θ_{vol} at 0.7 m depth ($P < 0.01$) for *Bromus* (29.5 $\pm$ 0.9 L and 4.5 $\pm$ 0.5%, respectively) compared with the native species (27.6 $\pm$ 1.1 L and 6.7 $\pm$ 0.9% for *Descurainia*, 23.3 $\pm$ 1.7 L and 11.9 $\pm$ 1.8% for *Vulpia*). Because the N × species and density × species interactions were also significant for all water use responses tested, single-df contrasts were tested to compare *Bromus* and the native species' sensitivities to N availability and plant density (Fig. 1). N availability had a greater effect on water use rate and total water use for stands of *Descurainia* ($P = 0.03$ and 0.01) and *Vulpia* ($P = 0.05$ and <0.01) compared with *Bromus*. This greater N effect for the native species was due to their lower mean responses at low N availability (Fig. 1). In addi-
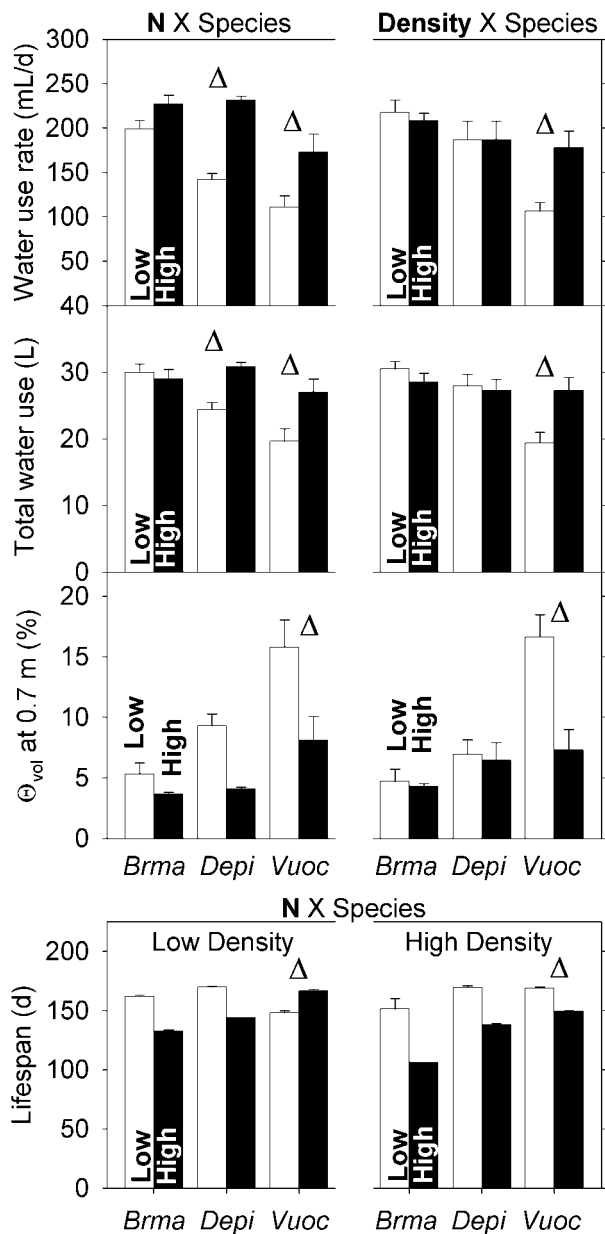
Fig. 1. Interaction plots for water use responses (top three panels) comparing sensitivities of *Bromus* and native species to N availability (N × species, left panels) and plant density (density × species, right panels). Water use responses are, from top panel: average rate of stand water use per day, total stand water use over the length of the experiment, and soil water content (Θ_{vol}) at 0.7 m soil depth at the end of the experiment. N sensitivity between species (N × species) for lifespan (bottom panels) was analyzed separately at low and high densities because the N × density × species interaction was significant. Significant differences in sensitivities to N availability or plant density between *Bromus* and each of the native species are denoted with Δ. White bars represent low levels and black bars represent high levels of N availability and plant density. *Brma* = *Bromus madritensis* subsp. *rubens*, *Depi* = *Descurainia pinnata*, and *Vuoc* = *Vulpia octoflora*. Bars are means + SE.

tion, *Vulpia* stands had lower water use rate, total water use, and higher Θ_{vol} at 0.7 m when density was low compared with *Bromus* stands ($P < 0.01$ for each species contrast between density levels, Fig. 1).

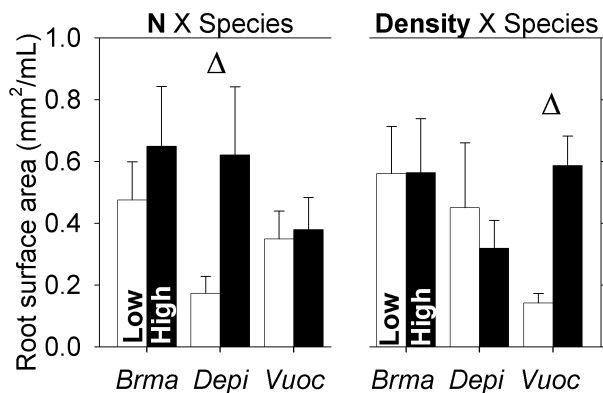Life span was analyzed in separate two-way ANOVAs (N

Fig. 2. Interaction plots for root surface area averaged over 0.3- and 0.7-m depths comparing sensitivities of *Bromus* and native species to N availability (N × species, left panel) and plant density (density × species, right panel). See Fig. 1 for symbols and species codes.

× species) at low- and high-density treatment levels because the species × N × density interaction was significant ($P < 0.01$, Fig. 1). Averaged over both levels of N availability, stands of *Bromus* senesced 10 d earlier than stands of either native species at low density and senesced 25 d and 30 d earlier than *Descurainia* and *Vulpia*, respectively, at high density (species effect for both levels of density, $P < 0.01$). While the sensitivity of life span to N fertilization was similar for *Bromus* and *Descurainia* at low and high density ($P = 0.19$ and 0.09, respectively), *Vulpia* stands lived longer at both low and high densities in part because *Bromus* senesced earlier at high N availability ($P < 0.01$ for each species contrast between N levels, Fig. 1).

Canopy leaf and root surface areas—Canopy leaf area and root surface area varied among species as well as between N availabilities and densities (all main effects, $P < 0.01$) but had little sensitivity to N availability and density. Canopy leaf area was greater at high than at low density (0.3 ± 0.06 m² vs. 0.1 ± 0.02 m²) and greater at high than at low N availability (0.3 ± 0.3 m² vs. 0.1 ± 0.1 m²). Canopy leaf area was greater for *Bromus* (0.26 ± 0.08 m²) and *Descurainia* (0.26 ± 0.07 m²) than for *Vulpia* (0.09 ± 0.03 m²), but species' sensitivities to N availability (species × N) and density (species × density) were not significantly different ($P = 0.84$ and 0.09, respectively). At 0.3-m soil depth, root surface area for *Vulpia* (0.4 ± 0.1 mm²/mL) was greater than either *Descurainia* (0.10 ± 0.05 mm²/mL) or *Bromus* (0.17 ± 0.05 mm²/mL), but *Bromus* and *Descurainia* had greater root surface area at 0.7-m depth (0.95 ± 0.16 mm²/mL and 0.65 ± 0.19 mm²/mL) compared with *Vulpia* (0.36 ± 0.11 mm²/mL, species × depth, $P < 0.01$). Averaged over soil depth, root surface area was lower for *Descurainia* than *Bromus* at low N availability ($P = 0.03$) and was lower at low density for *Vulpia* compared with that of *Bromus* (Fig. 2).

Leaf and root physiology—Average net assimilation and transpiration rates were greatest in *Descurainia*, followed by *Bromus* and then *Vulpia* ($P < 0.01$, species effects for both responses). Average net assimilation rates were 15.8 ± 0.54 μmol · m⁻² · s⁻¹ for *Descurainia*, 12.9 ± 0.52 μmol · m⁻² · s⁻¹ for *Bromus*, and 10.9 ± 0.36 μmol · m⁻² · s⁻¹ for *Vulpia*. Likewise, transpiration rates were 8.2 ± 0.35 mmol · m⁻² ·
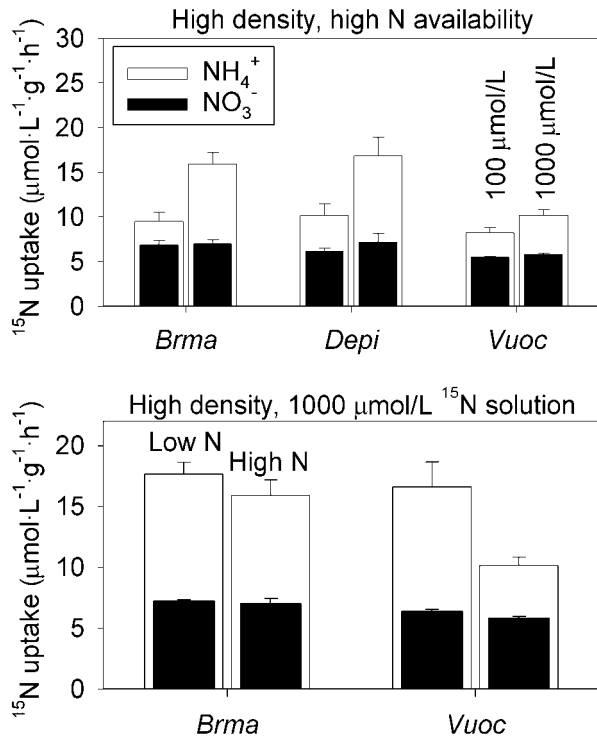
Fig. 3. ^{15}N uptake rates for *Bromus* and native species grown at high density and high N availability (upper panel) and for *Bromus* and *Vulpia* grown at high density and exposed to 1000 μmol/L ^{15}N solution (lower panel). White bars represent uptake rates of $^{15}NH_4^+$ and black bars represent $^{15}NO_3^-$. See Fig. 1 for species codes.
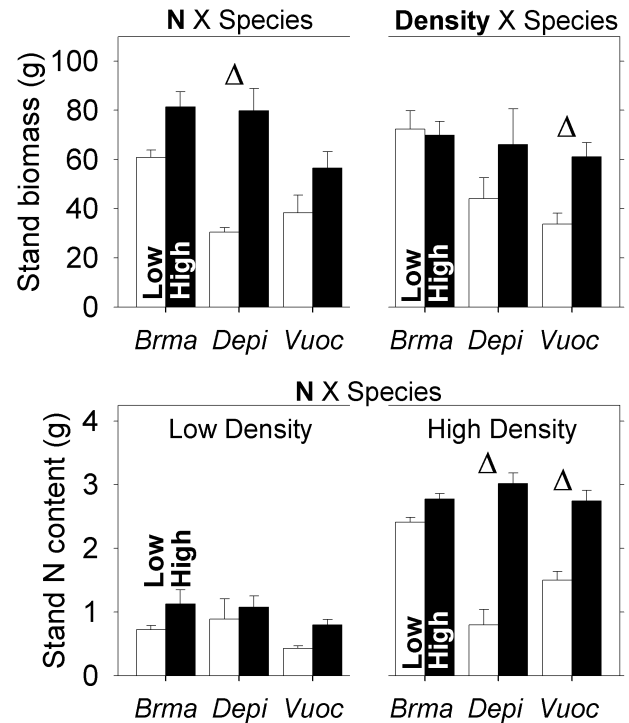

Fig. 4.   Interaction plots for stand biomass comparing sensitivities of *Bromus* and native species to N availability (N × species, upper left panels) and plant density (density × species, upper right panels). N sensitivity between species was analyzed separately at low and high densities (N × species) for stand N content (lower panels). See Fig. 1 for symbols and species codes.

s^{-1} for *Descurainia*, 5.9 ± 0.24 mmol · m^{-2} · s^{-1} for *Bromus*, and 4.4 ± 0.14 mmol · m^{-2} · s^{-1} for *Vulpia*. Net assimilation and transpiration rates were not significantly different between N levels (*P* = 0.25 and 0.88) or densities (*P* = 0.34 and 0.30). Sensitivities to N availability and density were not significantly different between *Bromus* and either native species.

Because root production for all species in the low-density treatment and for *Descurainia* at low N was insufficient for analysis of inorganic N uptake, the effects of N availability during growth (low vs. high), the form of inorganic N (NH_4^+ vs. NO_3^-), and incubation concentration of inorganic N (100 vs. 1000 μmol/L) were tested on a subset of the treatments. Considering only stands grown at high density and N availability (Fig. 3), *Bromus* and *Descurainia* had greater inorganic N uptake rates than *Vulpia* (species effect, *P* < 0.01). For all species, the increase in inorganic N concentration from 100 to 1000 μmol/L predominantly stimulated NH_4^+ uptake rates but had little effect on NO_3^- uptake (inorganic N concentration × inorganic N form, *P* < 0.01). Because of insufficient production of *Descurainia* roots, and only enough *Vulpia* roots for one inorganic N concentration, effects of growth N availability on N uptake could only be compared between *Bromus* and *Vulpia* at 1000 μmol/L concentration (Fig. 3). *Bromus* maintained high N uptake rates irrespective of growth N availability, whereas N uptake for *Vulpia* (primarily NH_4^+) decreased 30% with N fertilization (growth N availability × species, *P* = 0.04).

Stand biomass and N content—Stand biomass at final harvest was greater in *Bromus* compared with the native species.

Bromus produced 71 ± 4 g of biomass, whereas *Descurainia* and *Vulpia* produced 55 ± 9 g and 47 ± 5 g, respectively (species effect, *P* < 0.01). *Descurainia* had lower biomass at low N availability than *Bromus* (*P* < 0.01, Fig. 4), but sensitivities of *Vulpia* and *Bromus* to N fertilization were not significantly different (*P* = 0.50). In addition, *Vulpia* produced less biomass at low density compared with *Bromus* (*P* = 0.05), but the effect of density was not different between *Bromus* and *Descurainia* (Fig. 4, *P* = 0.22).

Total stand N content at final harvest was analyzed in separate two-way ANOVAs at each low- and high-density treatment level because species × N × density was significant (*P* < 0.01). At low density, total stand N was not significantly different among species (species effect, *P* = 0.06), and N availability had the same effect on *Bromus* stand N content as on *Descurainia* (*P* = 0.57) and *Vulpia* (*P* = 0.93, Fig. 4). At high density, however, total stand N for *Descurainia* and *Vulpia* were more sensitive to low N availability compared with *Bromus* (*P* < 0.01 and *P* = 0.02, respectively).

Biomass allocation between roots, shoots and reproduction—Root : shoot ratio was highest in *Bromus* (species effect, *P* < 0.01), but reproductive effort (seed mass divided by vegetative mass) was low compared with native annual species. *Bromus*' root : shoot ratio was 0.12 ± 0.01 g/g, followed by *Descurainia* (0.09 ± 0.01 g/g) and *Vulpia* (0.08 ± 0.01 g/g). These estimates fall within the ranges reported for winter annuals in North American warm deserts (Bell et al., 1979; Forseth et al., 1984). The effect of N fertilization on root : shoot ratios was not different between *Bromus* and each native species (Fig. 5). However, a significant density × species inter-
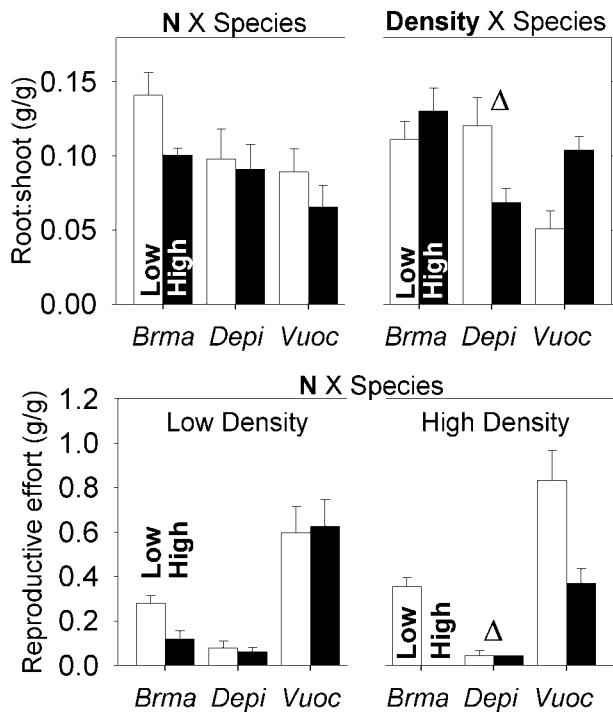
Fig. 5. Interaction plots for root : shoot comparing sensitivities of *Bromus* and native species to N availability (N × species, upper left panels) and plant density (density × species, upper right panels). N sensitivity between species was analyzed separately at low and high densities (N × species) for reproductive effort (lower panels). See Fig. 1 for symbols and species codes.

Fig. 6. Interaction plots for seed number and germination in separate analyses (N × species) at low (left panels) and high densities (right panels). See Fig. 1 for symbols and species codes.

action occurred ($P < 0.01$): *Descurainia* had a lower root : shoot ratio at high density compared with *Bromus* ($P = 0.01$). Reproductive effort was analyzed in separate ANOVAs at each density because the N × density × species interaction term was significant ($P = 0.05$). *Vulpia* had higher reproductive effort than either *Bromus* or *Descurainia* ($P < 0.01$ for both densities, Fig. 5). At low density, the effect of N availability was not different between *Bromus* and each of the native species. At high density, however, N fertilization reduced reproductive effort to a greater extent for *Bromus* than for *Descurainia* ($P = 0.02$).

Seed production, germination, and dormancy—*Bromus* produced fewer but larger seeds per individual plant compared with the native species. Seed production was analyzed separately for low and high plant densities (density × N × species interaction, $P = 0.01$; Fig. 6). *Bromus* produced the fewest seeds per plant at low and high plant densities (species effect, $P = 0.02$ and $P < 0.01$, respectively). At low density, species' sensitivities to N availability were not significantly different ($P = 0.09$) because of the enormous variation in seed number and the small sample size. At high plant density, the difference in seed production with N fertilization was not statistically different between *Bromus* and *Vulpia* ($P = 0.97$), but was significant between *Bromus* and *Descurainia* ($P = 0.02$): mean seed production per plant decreased to less than one seed for *Bromus* with N fertilization, while *Descurainia* more than doubled its seed production. Seed mass was greater for *Bromus* (1.48 ± 0.04 mg/seed) compared with *Descurainia* (0.07 ± 0.00 mg/seed) and *Vulpia* (0.39 ± 0.09 mg/seed, $P < 0.01$),
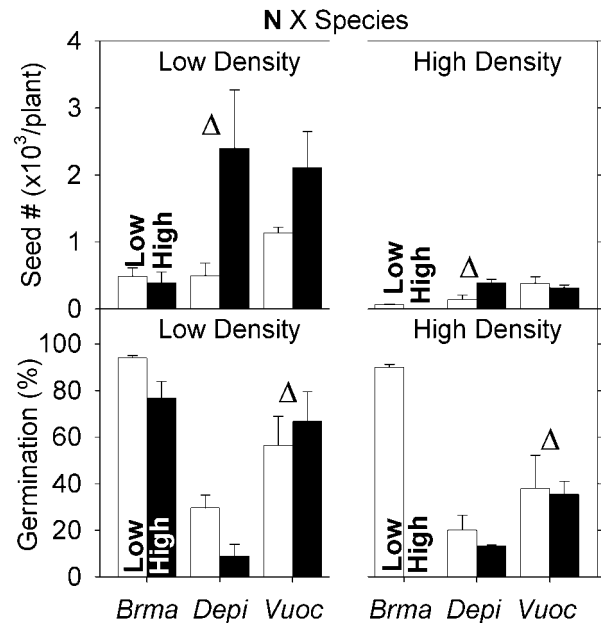
but the sensitivities of seed mass to N fertilization and plant density were not significantly different among species.

Germination was typically greater, and dormancy lower, in *Bromus* compared with the native species. Excluding the high density, high N treatment for *Bromus* (because production of seed was insufficient for analyses), germination was greatest for *Bromus* followed by *Vulpia* then *Descurainia* (species effect, $P < 0.01$, Fig. 6). Of the treatments that produced seed, dormancy of *Bromus* seeds was almost nonexistent (<1 ± 1%), and the natives had a significantly higher percentage of dormant seeds (42 ± 5% for *Descurainia*, 26 ± 5% for *Vulpia*) (species effect, $P < 0.01$). Interactions for N × species and density × species were not significant.

DISCUSSION

This study is the first to quantify traits that characterize the competitive potential of *Bromus madritensis* subsp. *rubens* compared with native Mojave Desert annuals. Stands of *Bromus* extracted soil moisture faster and had greater biomass and total N content than either *Descurainia* or *Vulpia*. This rapid resource use by *Bromus* is consistent with studies of other invasive annuals in western North America including *Bromus tectorum* in the intermountain West (Hulbert, 1955; Harris, 1967; Melgoza et al., 1990; Melgoza and Nowak, 1991), *Bromus* and *Avena* spp. in coastal sage scrub of California (Eliason and Allen, 1997), and brome grasses and forbs in California grasslands and woodlands (Gordon et al., 1989; Welker et al., 1991; Gordon and Rice, 1993, 2000). For *B. madritensis* subsp. *rubens*, greater resource uptake was likely a consequence of rapid root proliferation and greater root surface area. Interestingly, resource use was high for *Bromus* regardless of N availability or plant density. *Bromus* compensated for low density or low N availability by allocating biomass and N toward greater absorptive root surface area and by increasing N uptake.

Descurainia's overall slower rate of water extraction and its lower biomass and tissue N content than *Bromus* reflect its limited resource use at low soil N availability and its inability to acquire N under high plant densities. This sensitivity to low N explains why *Descurainia* is generally restricted to N-rich microhabitats including kangaroo rat mounds (Guo, 1998), subterranean termite-free mounds (Parker et al., 1982; Gutierrez and Whitford, 1987), N-enriched livestock areas (Nash et al., 1999), and beneath shrub canopies (Shmida and Whittaker, 1981; Parker et al., 1982; Samson, 1986; Guo, 1998; Brooks, 2000). The limitation of N on water use was not associated with lower transpiration rates (higher in *Descurainia* at both levels of soil N compared with those of *Bromus*). Canopy leaf areas were equally low for both *Bromus* and *Descurainia* at low soil N availability and therefore only partially explain *Descurainia*'s low water use at low soil N. Thus, *Descurainia*'s lower root-surface area also contributed to its slower rate of water extraction and lower N content compared with *Bromus*. Lower stand biomass for *Descurainia* compared with *Bromus* cannot be attributed to leaf-level differences in carbon gain because net assimilation rates were actually higher in *Descurainia*. However, leaves of *Descurainia* overlapped considerably in the canopy (L. A. DeFalco, personal observation), and self-shading may have resulted in lower carbon gain and hence less biomass production.

Resource use by the native grass *Vulpia* was lower than that of *Bromus* not only because of *Vulpia*'s sensitivity to low N availability (as observed for *Descurainia*), but also because of its lower resource use at low density. *Vulpia* was ineffective at extracting deep soil water despite its protracted lifespan and had lower total water use. This result for *Vulpia* was further exacerbated by lower rates of soil water use at low N and density compared with *Bromus*. Root-surface area was on average not different between *Bromus* and *Vulpia* at final harvest. Yet *Vulpia*'s conservative responses at the leaf level (lower net assimilation and transpiration rates) and stand level (smaller canopy leaf area) resulted in lower water use, biomass, and N content compared with the invasive *Bromus*. Native annuals such as *Vulpia* may have adapted to N-deficient soils by evolving slow growth rates compared with other native annuals and, thus, have less demand for N (Chapin et al., 1986; Gutierrez and Whitford, 1987; Chapin, 1991).

Bromus allocated biomass and tissue N to enhance soil water and N uptake, which may contribute to its ability to colonize and dominate diverse microhabitats, but this ability comes at the expense of reproductive output. For example, *Descurainia* and *Vulpia* generally produced greater numbers of seed over the different density and N treatments, although native seeds were much smaller than *Bromus* seeds. In fact, *Vulpia* had the lowest overall resource uptake but the greatest reproductive effort and seed production. Seed dormancy was almost nonexistent in *Bromus* because most of *Bromus*' seeds readily germinated. Seed dormancy allows desert annuals to escape unfavorable conditions (Cohen, 1966), and the investment of resources into the production of numerous, small seeds by the natives *Vulpia* and *Descurainia* are consistent with the "bet-hedging" strategy found in annual species from unpredictable environments (Brown and Venable, 1986; Philippi, 1993; Clauss and Venable, 2000). This strategy ensures that in years of high seedling mortality, a viable portion of seed remains in the seed bank to germinate in subsequent years that have more favorable conditions for germination and growth. Even though the larger seeds of *Bromus* may provide seedlings with resources necessary to improve their chances of establishment under unfavorable conditions (Baker, 1972; Wulff, 1986), its high germination fraction leaves *Bromus* susceptible to extended droughts that result in catastrophic mortality. Declines in *Bromus* and native Mojave Desert annuals are typical in years of low rainfall, and several years may pass after a drought before *Bromus* densities rebound to pre-drought levels, whereas natives usually recover more quickly (Hunter, 1991).

While the *potential* exists for *Bromus* to outcompete native annuals, it may not always displace native species in mixed annual communities. Native population densities are not always negatively correlated with the abundance of *Bromus* (Beatley, 1966; Hunter, 1991). Gutierrez and Whitford (1987) hypothesized that variability in soil N levels provides conditions for desert species with different N requirements to coexist. Furthermore, Mojave Desert annuals differ in their demand for N and adjust allocation among roots, shoots, and reproduction accordingly (Williams and Bell, 1981). Brooks (1999) concluded that *Bromus*' distribution was limited by N availability because it was found predominantly beneath shrub canopies and in ephemeral washes, where soil N was high, compared with shrub interspaces and hummocks, where soil N was typically low. Our results suggest *Bromus* has the capacity to thrive under conditions of high or low N availability and indeed is not as limited by low N compared with the two native species we studied. Thus, factors other than habitat partitioning based on N availability more likely account for the distribution and coexistence of native and non-native desert annual species. These factors include competition with other annual plant species (Inouye et al., 1980; Kadmon and Shmida, 1990; Pantastico-Caldas and Venable, 1993; Rice and Nagy, 2000), limiting resources other than N (Shachak et al., 1991), population regulation by drought (Hunter, 1991), preferential distribution of seeds beneath shrubs vs. interspaces (Nelson and Chew, 1977; Samson, 1986), density-dependent inhibition of germination (Inouye, 1980), and seed predation (Nelson and Chew, 1977; Inouye et al., 1980).

In summary, *Bromus* has the potential to dominate a diversity of landscapes within the Mojave Desert because it uses soil nutrients and water at a greater rate, in greater abundance, and over a wider range of soil N and plant densities compared with native annuals. However, the increased allocation toward resource acquisition comes at a cost to reproduction in *Bromus* and with a susceptibility to depletion of its seed bank during drought years. Understanding these allocation trade-offs and their associated environmental cues are paramount to predicting the long-term consequences of the interactions between native and non-native species and ensuring the success of the future management and control of *Bromus*.

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