Relationships of Native Desert Plants with Red Brome (*Bromus rubens*): Towards Identifying Invasion-Reducing Species

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The interactions between native and exotic species occur on a continuum from facilitative to competitive. A growing thrust in invasive species science is differentiating where particular native species occur along this continuum, with practical implications for identifying species that might reduce the invasibility of ecosystems. We used a greenhouse experiment to develop a competitive hierarchy of 27 native species with red brome, an invasive annual grass in southwestern USA arid lands, and a field study to assess *in situ* responses of brome to native perennial species in the Mojave Desert. Native species most competitive with brome in the competition experiment included the annuals pincushion and bristly fiddleneck and the perennials eastern Mojave buckwheat, sweetbush, and brittlebush that reduced brome biomass to 49 to 70% of its grown-alone amount. There was no clear difference in competitive abilities with brome between annual and perennial natives, and competiveness was not strongly correlated ($r = 0.15$) with the biomass of native species. In the field, sweetbush and brittlebush supported among the least cover of brome, suggesting congruence of the strong early competitive abilities of these species with *in situ* patterns of brome distribution. At the other extreme, brome attained its highest average cover (19%) below littleleaf ratany, significantly greater than all but three of the 16 species evaluated. Cover of brome was only weakly related ($r = 0.19$) to area of the perennial canopy, suggesting that factors other than the sizes of perennial plants were linked to differences in brome cover among species. Results suggest that (i) interactions with brome differ substantially among native species, (ii) these interactions are not as closely linked to biomass production as in more temperate regions, and (iii) there is potential for identifying native species that can reduce invasion of desert ecosystems.

Nomenclature: red brome, *Bromus rubens* L.; pincushion, *Chaenactis stevioides* Hook. & Arn.; bristly fiddleneck, *Amsinckia tessellata* A. Gray; eastern Mojave buckwheat, *Eriogonum fasciculatum* Benth.; sweetbush, *Bebbia juncea* (Benth.) Greene; brittlebush, *Encelia farinosa* A. Gray ex Torr.; littleleaf ratany, *Krameria erecta* Willd. ex Schult.

Key words: Competition, facilitation, plant-plant interactions, invasion-reducing communities, invasibility, revegetation.

Interactions between plants occur on a continuum. This continuum ranges from facilitation, where fitness of one or both species is enhanced, to competition, where the fitness of one or both is reduced (Keddy 2001; Brooker et al. 2008). Recently, interest in these interactions has grown in invasive species science for identifying native species and communities that are most competitive with exotic species and capable of reducing invasion (Levine et al. 2004; Thacker et al. 2009). If competition from native species is to effectively suppress exotic species, the native species must usurp resources (e.g., soil water or nitrogen) required by an exotic, occupy space (e.g., regeneration microsites) otherwise inhabitable by an exotic, exude allelopathic chemicals or negatively modify sites, interfere with reproduction or emergence from the soil seed bank, or reduce fitness through other means (Seabloom et al. 2003). For these purposes, competition is broadly defined as any reduction in the fitness of exotic species due to the presence of native species (Fowler 1986).

Several experiments have demonstrated that species composition of resident communities is a key factor affecting the competitive (or facilitative) environment to which a potential invader is exposed (Brown et al. 2008). Species differ in traits such as height, biomass, growth rate, and root:shoot ratio that are related to a species' ability to capture resources and are linked to competitive ability (Booth et al. 2003). The particular traits that confer competitive or facilitative advantages across different communities (e.g., arid versus temperate ecosystems) are generally not well articulated, making it difficult to accurately predict which native species might be the most competitive with exotic species (Barney et al. 2005). Assessing species interactions in trait- and species-rich communities also requires many pair-wise comparisons, making it difficult to test more than a few species. One approach to screening the competitive abilities of many species is to grow all species of interest with the same species, termed a "phytometer"

(Keddy 2001). Keddy et al. (2002) used this approach to compare the competitive abilities of 63 herbaceous species from temperate eastern Ontario. Competitive abilities were hierarchical, with native species reducing phytometer biomass by 45 to 99%. A potential disadvantage of using a phytometer to screen competitive ability is that competition is only determined against the phytometer species. However, this is a strength precisely when competitive ability against a particular species is of interest, such as native species versus a target exotic species.

Exotic grasses such as red brome (*Bromus rubens* L., hereafter *Bromus*) infest extensive areas of southwestern arid lands including the Mojave Desert. These exotic species have increased fuel loads, facilitating widespread fires in desert ecosystems not thought to have burned extensively prior to the widespread establishment of these species by the mid-1950s (Salo 2005). For example, more than 2% of the entire area of the Mojave Desert burned in 2005 alone following a moist year that stimulated vigorous annual plant growth (Brooks and Matchett 2006). These fires kill late-successional perennial vegetation, often reducing perennial cover for ≥ 40 years and altering native species composition for indeterminate time periods (Abella 2010). The extensiveness of invasion across millions of hectares in the arid West makes reducing dominance of exotic grasses a challenging task confronting resource managers. A complicating factor is that some native perennial species may actually facilitate the establishment and growth of exotic plants by forming fertile islands high in soil nutrients and with ameliorated microclimates (Brooks 2009; Craig et al. 2010).

It is not well known where different native annual and perennial species fall on the continuum of facilitative to competitive with exotics such as *Bromus* in southwestern arid lands, or if competition from native species is an effective management tool for reducing exotic plants (Abella and Newton 2009). The objectives of this study were to: develop a *Bromus* competitive hierarchy under controlled greenhouse conditions with a range of species native to the Mojave Desert, and to assess *in situ* patterns of *Bromus* cover below native perennial species. We posed the following questions: (1) Can native desert annual and perennial species be arranged in a competitive hierarchy with *Bromus*? (2) Are interactions of native species with *Bromus* correlated with species traits such as root mass? (3) Does *Bromus* cover vary in the field among native perennial species, and do these results support those of the competition experiment? We hypothesized that all native species would reduce the growth of *Bromus* in the competition experiment, but the relative reduction would vary among species. Based on studies such as Keddy et al. (2002), we further hypothesized that the strongest competitors with *Bromus* are species that grow the most rapidly and produce the greatest biomass. We suspected that, owing to rapid biomass production, annuals as a group would be more competitive than perennials. We also anticipated that the poorest perennial competitors at the seedling stage in the competition experiment would be the most heavily infested by *Bromus* in the field.

Materials and Methods

Autecology of the Study Species. *Bromus* is native to southern Europe, northern Africa, and southwestern Asia, occurring from sea level to 1,300 m in arid to mesic shrubland and steppe habitats (Brooks 2000). *Bromus* readily invades disturbed habitats in arid southwestern North America, but it also infests relatively undisturbed late-successional communities such as those containing creosote bush (*Larrea tridentata* (DC.) Coville) and blackbrush (*Coleogyne ramosissima* Torr.; Salo 2005). In southwestern arid lands, *Bromus* forms prodigious soil seed banks that can exceed 3,000 seeds/m^2 (0 to 5 cm soil depth) and are readily germinable given moisture and warm spring temperatures (Abella et al. 2009a). *Bromus* often is most abundant below the canopies of native perennial plants, although it can dominate interspaces during wet years and on sites with favorable soils (Brooks 1999). In the Mojave Desert, for example, Brooks (2003) reported that the aboveground biomss of *Bromus* in interspaces averaged < 0.5 g m^{-2} in 1996 (a dry year) and 5 g m^{-2} in 1997 (a moister year). In contrast, biomass below perennials was 10 g m^{-2} in 1996 and 55 g m^{-2} in 1997, approximately 10- to 20-fold greater than in interspaces. *Bromus* is considered one of the most abundant and widespread annual species across the Mojave Desert (Beatley 1966; Hunter 1991; Brooks 2009).

Study Area. Our work focused on species inhabiting the Mojave Desert, a 124,000-km^2 hot desert of southeastern California, southern Nevada, southwestern Utah, and western Arizona in the southwestern USA (Rundel and Gibson 1996). A weather station (Las Vegas, NV, elevation 662 m) typifying the eastern Mojave Desert has reported averages of 11 cm yr^{-1} of precipitation, July daily maximum temperature of 40^{o}C, and January daily minimum temperature of 1^{o}C (1937 to 2009 records; Western Regional Climate Center, Reno, NV). This desert receives > 60% of its rainfall in winter, facilitating peak biomass of both native and exotic annual plants in late spring (March through May) during moist years (Beatley 1974). Seedlings of many native perennials also germinate during this period, with growth of the seedlings and mature plants occurring primarily during the warm spring and summer months (Turner and Randall 1987). The typical physiognomy of the desert is widely spaced native perennial plants, such as *Larrea tridentata* and white bursage (*Ambrosia dumosa* (A. Gray) Payne), with interspaces between the shrubs containing annual plants (in moist years) or sparsely vegetated soil.

Competitive Hierarchy Experiment. Following Keddy et al. (2002) for developing competitive hierarchies, we selected 35 species native to the Mojave Desert that ranged widely in growth form (16 annual forbs, 3 perennial grasses, 7 perennial forb-subshrubs, and 9 perennial shrubs), longevity (16 annuals and 19 perennials), and successional affiliation based on Abella (2010). Nomenclature and growth form and longevity classification follow NRCS (2010). We obtained seed[1,2] of the native species from the plant nurseries of Lake Mead National Recreation and the Las Vegas Springs Preserve, both within the Mojave Desert. We collected *Bromus* seed from two populations within Lake Mead National Recreation Area. We conducted a pilot emergence assay (one month duration, with 20 seeds sown in one 3.8-L pot per species with the same soil to be used in the experiment) to determine seed emergence rates to estimate the number of seeds needed to be sown to produce the desired density for the competition experiment.

Based on the emergence information, we sowed seeds of native species for the competition experiment in separate pots to attain a density of 5 seedlings per pot (278 m^{-2}). We simultaneously sowed seeds of the *Bromus* phytometer in the same pots containing the native species to also attain a density of 5 seedlings per pot for *Bromus*. Due to the large number of species tested, we were only able to assess a single density. This density, however, is within the range reported for Mojave Desert field sites in years that have precipitation patterns supporting *Bromus* growth (Beatley 1966; Hunter 1991). To try and ensure close contact of natives with *Bromus*, we used 3.8-L pots that were circular with a diameter of 15 cm. We filled pots with a sterile soil mix consisting of 2:1 sand:potting soil[3] to simulate the sandy loam textures within ranges commonly characterizing Mojave Desert soils (Lato 2006). Our target was to have three replicate pots for each native species, so we sowed seeds in four pots in case some pots lacked sufficient seed germination to attain the target density. We also grew 5 seedlings per pot of brome alone in 10 replicate pots. We randomly arranged pots on a bench in a greenhouse maintained at 24°C without supplemental lighting. Pots were watered with a misting system in operation for two minutes each day that delivered 1.5 cm of water per day.

We initiated the experiment in April 2009, when *Bromus* actively grows in the field (Beatley 1966), and ran the experiment for eight weeks. Each week, we measured the heights of native and *Bromus* plants and counted the number of plants per pot, thinning plants to the target density of 5 plants per pot as needed. At the end of the experiment, which was the time of senescence of *Bromus* and the native annuals, we harvested above- and below-ground biomass by species within pots and determined oven-dry weight by heating at 70°C for 24 h. Since we averaged data from all plants by species within pots, distinguishing root masses (which could become intertwined by growing in close contact) of individual plants within species was not necessary.

Despite the pilot study and oversowing many species, eight species failed to attain the target density in at least three replicate pots and were not further included in the experiment. While it is possible that manipulating seeds could have increased germination and emergence, we chose to minimally manipulate seeds and avoid attempting species-specific treatments that could have confounded among-species comparisons of competitive abilities. For example, gibberellic acid may have enhanced germination of some species, but this treatment can affect subsequent seedling growth (Baskin and Baskin 2001). A total of 27 species, 12 annuals and 15 perennials, had sufficient emergence for inclusion in the experiment.

Field Patterns of *Bromus* below Native Perennials. We used seven sites, located in Lake Mead National Recreation Area, Red Rock Canyon National Conservation Area, and surrounding

Bureau of Land Management land in southern Nevada in the eastern Mojave Desert, to assess the cover of *Bromus* below native perennial species. We selected these sites because they contained a variety of perennial species to permit within-site comparisons and harbored some of the species included in the competition experiment. These sites also contained *Bromus* infestations, which we identified based on a landscape-scale assessment of invasive species distributions in the study area (Abella et al. 2009b). Elevations of the sites ranged from 710 to 1,367 m. The sites were in the 421, 731, 732, and 750 mapping units of the Clark County soil survey and were primarily classified as loamy-skeletal, carbonatic, mesic, shallow Calcic Petrocalcids and Typic and Lithic Torriorthents (Lato 2006). These soils have gravelly loam and sandy loam textures (Lato 2006). Sites had a geographic extent of 64 km, spanning the Universal Transverse Mercator coordinates of 642,316 m E, 4,001,353 m N and 702,253 m E, 3,981,227 m N (zone 11, North American Datum 1983).

At the center of each site within an area of 1 ha, we established four belt transects (one in each of the cardinal directions) that were 5 m wide and up to 50 m long. Along each transect, we measured the first two individuals of any perennial species intended to be included in the competition experiment. We required that an individual have a developed canopy (which excluded sampling seedlings of these species) that did not overlap with the canopy of any other perennial species. We measured the perimeter of each individual canopy (at its greatest extent) and calculated canopy area from perimeter using the formula for a circle to approximate the shape of the canopies. In a vertical plane to the ground below canopies, we visually categorized areal cover of *Bromus* below each perennial plant using the following cover classes: 0 = 0% cover, 1 = > 0 < 1%, 2 = 1 to 3%, 3 = 3 to 6%, 4 = 6 to 12%, 5 = 12 to 25%, 6 = 25 to 50%, 7 = 50 to 75%, and 8 = 75 to 100%. Two interspaces (defined as an area ≥ 1 m from the nearest perennial plant canopy) were also identified using random coordinates within each transect and sampled in the same manner. The dimensions to be sampled within the interspaces were determined based on the dimensions of two randomly selected perennials measured in transects. *Bromus* was the predominant standing annual at all sites, although at one site small amounts of the exotic annual grasses *Schismus* spp. and cheatgrass (*Bromus tectorum* L.) were intermingled with the *Bromus* stalks. These species were included in the *Bromus* cover estimates, as the mat of plant matter at this site was difficult to partition into the small amounts of the other species. Because of *Bromus*'s contribution to hazardous fuels, standing dead biomass is as important as green biomass. We made measurements from November 2009 to January 2010 when *Bromus* was not actively growing and sampled standing dead biomass as a measure of recent accumulated biomass. Dead *Bromus* plants can persist for more than two years (Beatley 1966).

Data Analysis. For the competition experiment, we calculated native species performance versus *Bromus* as the percent of grown-alone biomass that *Bromus* attained when grown with a native species (Equation 1).

(*Bromus* biomass when grown with a native species/*Bromus* grown-alone biomass) × 100 [1]

Because data did not meet assumptions of homogeneity of variance and normality, we compared performance among species using a nonparametric Kruskal-Wallis test followed by Tukey's test ($\alpha = 0.05$) for multiple comparisons in SAS software (PROC NPAR1WAY, followed by PROC MIXED on the ranks; SAS Institute 1999). Since the original data were continuous, we report means and standard errors of the means for interpretive purposes but present the nonparametric statistical results. We used Pearson correlation coefficients, as Spearman rank coefficients were similar, to examine relationships among *Bromus* and native species traits. Traits included root and shoot length, and root, shoot, and total biomass for mono-specific and mixed-species pots. All values in the experiment were averaged on a pot basis and expressed as averages per plant, and were further averaged on a native species basis for analyses at the among-species level.

Despite selecting mixed-species sites for the field study, no site contained all of the species that were included in the competition experiment and species composition of the sites was not identical. Because of this, we viewed the sites and transects as frameworks in which to sample within a defined area, and each perennial plant as a discrete individual unit for analysis. In a non-parametric analysis to accommodate the categorical cover data, we compared the median percent cover (based on midpoints of cover classes) among perennial species and interspaces with a Kruskal-Wallis test followed by Tukey's test for multiple comparisons (SAS Institute 1999). Confidence intervals at the 95% level were computed through the PROC UNIVARIATE and CIQUANTDF option routine.

Results

Competition Experiment. *Bromus* root, shoot, and total plant mass were strongly correlated, with correlation coefficients (Pearson r) ranging from 0.84 to 0.97 when *Bromus* was grown with native species. Root length and root mass ($r = 0.75$) and shoot length and shoot mass ($r = 0.85$) also were strongly correlated. Based on these relationships, we assessed competitive effects of natives on *Bromus* using *Bromus* total plant (root + shoot) biomass.

There was an overall effect of native species identity on *Bromus* biomass indicated by a significant Kruskal-Wallis test (χ^2 statistic = 41.9; $P = 0.0336$), but P-values were > 0.06 in pairwise multiple comparisons among species. We arranged species hierarchically based on their mean effects on *Bromus* biomass. The strongest native annual competitors versus *Bromus* included pincushion (*Chaenactis stevioides* Hook. & Arn.), bristly fiddleneck (*Amsinckia tessellata* A. Gray), cleftleaf wildheliotrope (*Phacelia crenulata* Torr. ex S. Watson), and desertbells (*Phacelia campanularia* A. Gray), which reduced *Bromus* biomass to 50 to 78% of its grown-alone amount (Fig. 1). By reducing *Bromus* biomass to 49 to 70% of grown-alone amount, the strongest native perennial competitors were eastern Mojave buckwheat (*Eriogonum fasciculatum* Benth.), sweetbush (*Bebbia juncea* (Benth.) Greene), and brittlebush (*Encelia farinosa* A. Gray ex Torr.). Several species, such as the annual California poppy (*Eschscholzia californica* Cham.) and perennials desert marigold (*Baileya multiradiata* Harv. & A. Gray ex A. Gray), big galleta (*Pleuraphis rigida* Thurb.), and brownplume wirelettuce (*Stephanomeria pauciflora* (Torr.) A. Nelson), promoted greater *Bromus* biomass than when *Bromus* was grown alone. The average competitive performance of native species was not strongly correlated (r = 0.15) with the mean total biomass per plant (root + shoot) they attained. The correlation also was weak (r = 0.24) when considered on a pot basis rather than averaging across native species.

***Bromus* Cover below Native Perennials.** A total of 56 interspaces and 319 individuals of 16 species were measured. The median cover of *Bromus* below perennial plants differed significantly among species and interspaces (Kruskal-Wallis χ^2 = 144; $P < 0.0001$). Interspaces contained the lowest median *Bromus* cover, significantly lower at $P < 0.05$ than 10 of 16 (63%) of the perennial species studied (Table 1). Species were arranged hierarchically with respect to

Bromus cover, with turpentinebroom (*Thamnosma montana* Torr. & Frém.), *Bebbia juncea*, Virgin River brittlebush (*Encelia virginensis* A. Nelson), Mexican bladdersage (*Salazaria mexicana* Torr.), and *Encelia farinosa* exhibiting lower tier medians. Littleleaf ratany (*Krameria erecta* Willd. ex Schult.), Torrey's jointfir (*Ephedra torreyana* S. Watson), *Larrea tridentata*, and cheesebush (*Hymenoclea salsola* Torr. & A. Gray) harbored among the greatest *Bromus* cover among species. *Krameria erecta* had a median twice as high as the next highest species and supported significantly greater *Bromus* cover than all but three of the other species.

Bromus cover was not strongly correlated with the area of a perennial plant canopy (r = 0.19) when all 319 individual plants were included. *Bromus* cover-perennial canopy area correlations also were not strong within species. For example, the correlation was only 0.14 for *Krameria erecta* and 0.16 for *Encelia farinosa*.

Discussion

Evidence for Hypotheses. In contrast to our expectation that all native species would reduce *Bromus* biomass by some extent in the competition experiment, *Bromus* actually exhibited greater amounts of biomass (than when grown alone) when grown with species such as *Stephanomeria pauciflora*, *Pleuraphis rigida*, and *Eschscholzia californica* (Fig. 1). These results contrast with those of Keddy et al.'s (2002) competitive hierarchy experiment with temperate eastern North American species, where all 63 species reduced biomass of the native annual phytometer, fluxweed (*Trichostema brachiatum* L.). Since experimental designs were similar between the studies, our contrasting findings could result from the exotic versus native phytometer or reflect that desert species are not as strongly competitive as temperate species.

Also contrasting with our hypothesis, biomass production and plant size of native species was not strongly related to competitive ability in the greenhouse or to the amount of *Bromus* cover the native species supported in the field. Competitive ability in temperate regions frequently is related to plant size (Keddy 2001). Keddy et al. (2002), for instance, found that total and above- or below-ground biomass were most strongly correlated ($r = 0.53$ to 0.58) with competitive performance. Plant size in our study also was not linked to facilitation of *Bromus* in the field, as species such as *Krameria erecta* supporting the greatest *Bromus* cover were not necessarily the largest. Similarly, competitive performances of annual and perennial species overlapped (Fig. 1), incongruent with our supposition that annuals would outperform seedlings of perennial plants. Other traits than plant size and annual/perennial status apparently are more closely connected to outcomes of interactions with *Bromus*.

The results of the correlative field study of *Bromus* cover below perennial species followed those of the greenhouse competition experiment more closely for some species than others. *Eriogonum fasciculatum*, the top competitor with *Bromus* in the greenhouse, harbored varying amounts of *Bromus* in the field to exhibit a middle ranking among species (Table 1). Considering the next three top competitors in the greenhouse, *Bebbia juncea* and *Salazaria mexicana* supported lower tier amounts of *Bromus* cover in the field, and *Encelia farinosa* low-middle amounts. *Larrea tridentata*, *Ambrosia dumosa*, and *Hymenoclea salsola* ranked in the middle in greenhouse competitive performance, and supported middle-high amounts of *Bromus* in the field. *Pleuraphis rigida*, the least competitive species in the greenhouse that also was part of the field study, ranked in the middle among species in the field. A longer term field experiment tracking interactions with *Bromus* of planted perennials from the seedling through adult stages could be useful for evaluating how competitive interactions might change through species' life cycles.

Comparing Species Performance. Brooks (2009) is the only other study known to us that has compared relationships in the native species versus *Bromus* direction (as opposed to *Bromus* effects on natives) among an array of species in southwestern deserts. Brooks (2009) compared *Bromus* biomass below 29 native perennial species in the southwestern Mojave Desert. While not all species were the same between Brooks (2009) and our study, the large numbers of species included in the studies enabled a relative ranking of species relationships with *Bromus*. We were able to compare 10 species in Brooks (2009) that were included in our field study, six of which also were included in our greenhouse experiment. Within the studies, we ranked these 10 species relative to all species included in a respective study (27 in our greenhouse experiment, 16 in our field study, and 29 in Brooks [2009]) into lower, middle, and upper thirds in their performance versus *Bromus*.

Eight of the 10 species were within one performance category among studies, while two species differed substantially (Table 2). For example, *Bebbia juncea* consistently ranked as 'good' for both reducing *Bromus* in the greenhouse and supporting low amounts of *Bromus* cover in our and the Brooks (2009) field studies. *Eriogonum fasciculatum* ranked as 'good' in the greenhouse and 'medium' in the two field studies, and *Ambrosia dumosa* consistently ranked as 'medium'. Species that ranked 'poor' in our field study, such as *Krameria erecta*, ranked no better in Brooks (2009) than 'medium'. *Salazaria mexicana* and *Thamnosma montana* were the most disparate species, ranking 'good' in our study, but 'poor' in Brooks (2009).

Variability was high in performance among individuals within a species in both our studies and Brooks (2009), where standard errors of the means were as large or nearly as large as means for several species. Brooks (2009) highlighted two major spatial scales of variability in native species relationships with *Bromus*: broad landscape scales such as elevation gradients, where *Bromus* is typically most abundant at middle elevations, and within-site variation where microsites such as interspaces and canopies of perennial plants are important. He further noted that *Bromus*-native species relationships can shift with elevation. For example, *Bromus* may be closely associated with *Larrea tridentata* at lower elevations, but as abundant or more abundant in interspaces or below perennials other than *Larrea* at cooler and moister higher elevations. Further evaluating the potential interactions of landscape gradients (e.g., elevation) with perennial plants in affecting the distribution of *Bromus* could be useful future research.

Species Traits and Performance. While we did not find that the traits of biomass production in the greenhouse experiment or plant size in the field study were correlated with native species performance versus *Bromus*, other traits could be important. Some of the many traits of potential importance for perennials could include: seasonality of growth, canopy morphology, life span, degree and nature of fertile island formation, successional affiliation, literfall and decomposition, allelopathy, and rooting habit/mycorrhizal associations. For example, in a Mojave Desert field experiment, James et al. (2006) reported that the seasonality of growth of the native shadscale saltbush (*Atriplex confertifolia* (Torr. & Frém.) S. Watson) more closely corresponded with that of the exotic annual Arabian schismus (*Schismus arabicus* Nees) and was a better competitor with *Schismus* than the perennial Parry's saltbush (*Atriplex parryi* S. Watson). De Soyza et al. (1997) found that differences in canopy morphology among *Larrea tridentata* individuals influenced microclimates and associated native annual communities. This observation suggests that differences in canopy morphology both within and among species could influence the growing environment for *Bromus*. Based on observing distributions of native annuals in the Mojave Desert, Muller (1953) suggested that perennials with shorter life spans harbored fewer annuals. This supposition appears consistent with our field data for some species but not others. For instance, *Bebbia juncea* supported little *Bromus* cover and was classified by Bowers et al. (1997) as a short-lived perennial with an estimated maximum life span of 20 years. However, *Eriogonum fasciculatum* and broom snakeweed (*Gutierrezia sarothrae* (Pursh) Britton & Rusby) also are considered short lived with estimated life spans of 20 years, but these species harbored intermediate amounts of *Bromus*. In addition to other traits, life span could influence the degree and nature of fertile island formation (Holmgren et al. 1997). Thompson et al. (2005) showed that soil properties such as nitrogen mineralization differed below canopies of three late-successional shrub species in the northern Mojave Desert. It could be hypothesized that species with shorter life spans, often with early successional affiliations (Bowers et al. 1997), do not form well-developed fertile islands and hence would be less favorable for *Bromus* growth. The five species that harbored the least amount of *Bromus* in our field study (Table 1) all are considered as early successional based on Abella's (2010) successional classification of Mojave Desert species. With the exception of *Hymenoclea salsola*, species that supported the greatest cover of *Bromus*, such as *Krameria erecta* and *L. tridentata*, are classified as late successional.

Litterfall, allelopathy, and rooting habit/mycorrhizal associations could further influence the growing environment for *Bromus* near perennial plants. Strojan et al. (1979) reported that yearly litterfall amounts in grams per shrub varied by an order of magnitude among six shrub species in the northern Mojave Desert. Depending on decomposition rates, this variation in litterfall could result in different thicknesses of litter layers below shrubs, which could positively or negatively or not influence *Bromus* establishment. Gray and Bonner (1948) isolated an allelopathic growth inhibitor in the foliage of *Encelia farinosa*, which was observed to harbor few annual plants. However, Muller (1953) subsequently found that an even stronger growth inhibitor was present in *Ambrosia dumosa*, a species that harbored abundant annuals. The significance of allelopathy as a factor influencing annuals below perennials remains unclear. The possible role of rooting habit also is unclear. Wallace et al. (1980) reported that *Krameria erecta* had more than twice the proportion of fine roots (of its total root system) in the upper 10 cm of soil among nine perennial species in the northern Mojave Desert. It could be hypothesized that this shallow rooting intensifies competition against shallow-rooted annuals, yet *K. erecta* harbored the greatest cover of *Bromus* in our field study (Table 1). Since *K. erecta* also can be a root parasite on other perennial plants (Griffith 1991), which could influence nutrient contents in soils below its canopy, these observations suggest that exploring the possible influence of rooting ecology in *Bromus*-native species relationships may be a useful topic for future research. Similarly, Titus et al. (2002) reported that *Baileya multiradiata* had the greatest concentration of arbuscular mycorrhizae among 15 Mojave species. *Baileya multiradiata* was one of the species that facilitated *Bromus* growth in the greenhouse experiment (Fig. 1), and it is unclear if mycorrhizal associations influence interactions with *Bromus*.

While traits such as fertile island formation may be less important in native annual species interactions with *Bromus*, other traits such as seasonality of growth, water requirements, and resource use discussed above for perennials may also be important for annuals (e.g., DeFalco et al. 2003). In addition, the potential interaction of perennial plants with associated native annual communities in influencing relationships with *Bromus* should be examined. For example, the most competitive native vegetation with *Bromus* could be a competitive perennial species paired with native annuals most competitive with *Bromus*, if such native vegetation types exist.

Feasibility of Native Species Treatments. Since early work in the 1940s and 1950s (Went 1942; Muller 1953; Muller and Muller 1956) and with few exceptions such as Brooks (2009), little research has been directed at among-species differences in associations with annual species in southwestern deserts. This early work also concentrated on associations with native annuals, with less emphasis on exotics like *Bromus*. Much contemporary work has further focused on the effects of exotic annuals on native species, rather than which native species most strongly influence exotics. As a result, little research is available to help identify which native species could be amenable to control strategies for *Bromus* and whether competition from native species is a feasible treatment for reducing exotic plants.

For competition by native plant species to be an effective treatment for controlling exotics, the native species must: (1) compete with and reduce the exotic, (2) become reliably established via seeding or planting on sites where the exotic grows, and (3) be amenable to propagation and plant material development so that sufficient quantities of the species is available for treatments at operational scales. Native species treatments have shown mixed success at reducing exotic plants, either in the context of oversowing the native into an existing stand of the exotic, or following treatment of the exotic by herbicide or other methods. For example, Bakker and Wilson (2004) found that seeding a mixture of native species reduced the number of plots invaded by the exotic perennial grass crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.) by 33% in Saskatchewan grasslands. Similarly, oversowing the native annual forb firewheel (*Gaillardia pulchella* Foug.) into existing stands of the exotic annual forb bastardcabbage (*Rapistrum rugosum* (L.) All.) reduced productivity of the exotic by up to 72% along Texas roadsides (Simmons 2005). However, neither Thacker et al. (2009) nor Stevens and Fehmi (2009) found that seeding native perennial grasses reduced exotic grasses (including *Bromus tectorum* and buffelgrass [*Pennisetum ciliare* (L.) Link]) of southwestern arid lands. In contrast, Seabloom et al. (2003) found that seeding native perennial grasses into California exotic annual grasslands (including species of *Bromus*) reduced seed production and biomass of the exotics.

Further work for evaluating native species treatments is required in deserts where facilitation of exotics by native species appears prevalent (Rodríguez-Buriticá and Miriti 2009). Indeed, we found that *Bromus* had greater growth when grown with natives (compared to when *Bromus* was grown alone) for more than half of the native species in our greenhouse competition experiment, and none of the 16 native perennial species in the field study harbored less cover of *Bromus* than interspaces. These findings suggest that ascertaining native species that at the very least facilitate *Bromus* the slightest may be a reasonable goal for identifying native vegetation types less susceptible to *Bromus* invasion.

Sources of Materials

[1]Las Vegas Springs Preserve, 333 S. Valley View Blvd., Las Vegas, NV 89107.

[2]National Park Service, Lake Mead National Recreation Area, 601 Nevada Way, Boulder City, NV 89005.

[3]Kellogg Potting Soil, Kellogg Garden Products Corporate Office, 350 W. Sepulveda Blvd., Carson, CA 90745.

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Table 1. Median percent cover of *Bromus rubens* in interspaces and below native perennial plants (arranged in order of supporting the least to the most *Bromus*) in the eastern Mojave Desert, southwestern USA. Medians without shared letters differ at $P < 0.05$ (Tukey's test).

Microsite	Median	95% CI[a]	n[b]
Interspace	1 a	1-2	56
Thamnosma montana	2 ab	2-5	22
Bebbia juncea	2 abc	0-9	7
Encelia virginensis	2 abc	1-19	7
Salazaria mexicana	2 abc	2-9	9
Encelia farinosa	3 bc	2-5	30
Coleogyne ramosissima	5 abc	2-5	40
Pleuraphis rigida	5 abcd	2-9	6
Menodora spinescens	5 bc	5-5	37
Psorothamnus fremontii	5 bc	2-9	29
Ambrosia dumosa	5 c	5-9	22
Eriogonum fasciculatum	5 bc	2-38	11
Gutierrezia sarothrae	5 bc	2-9	11
Hymenoclea salsola	9 bcd	2-38	10
Larrea tridentata	9 bcd	2-38	13
Ephedra torreyana	9 c	5-19	28
Krameria erecta	19 d	19-19	37

[a] Lower and upper bounds of confidence intervals for medians.

[b] Total number measured at seven sites.

Table 2. Summary of the performance of native perennial species with *Bromus rubens* in this study compared with Brooks (2009), Mojave Desert, southwestern USA. Species were ranked as poor, medium, or good in their ability for reducing *Bromus* biomass (greenhouse competition experiment) and for supporting low amounts of *Bromus* in the field (i.e. a 'good' rating indicates that *Bromus* is sparse below a species' canopy).

Species	This study: competition	This study: field	Brooks (2009): field
Ambrosia dumosa	Medium	Medium	Good
Bebbia juncea	Good	Good	Good
Coleogyne ramosissima	—	Medium	Medium
Eriogonum fasciculatum	Good	Medium	Medium
Hymenoclea salsola	Medium	Poor	Medium
Krameria erecta	—	Poor	Medium
Larrea tridentata	Medium	Poor	Medium
Psorothamnus fremontii	—	Medium	Poor
Salazaria mexicana	Good	Good	Poor
Thamnosma montana	—	Good	Poor

Fig. 1. Competitive hierarchy of native Mojave Desert species with *Bromus rubens*. Competitive performance is calculated as the percentage of the biomass *Bromus* attained with native species compared to when *Bromus* was grown alone. Low values indicate strong competitive effects of native species on *Bromus*. Error bars are 1 SE of the mean.

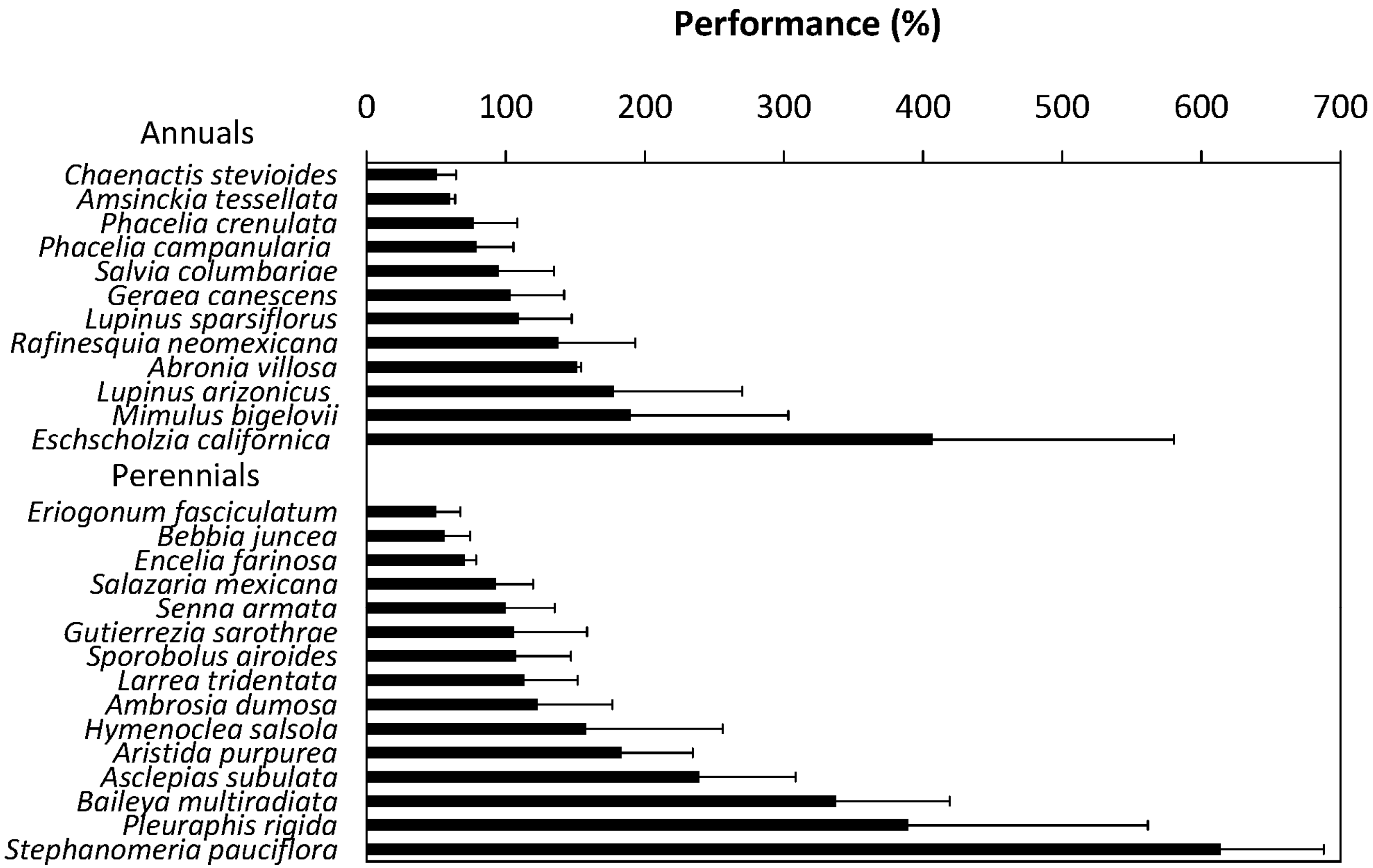
Performance (%)
0
100
200
300
400
500
600
700
Annuals
Chaenactis stevioides
Amsinckia tessellata
Phacelia crenulata
Phacelia campanularia
Salvia columbariae
Geraea canescens
Lupinus sparsiflorus
Rafinesquia neomexicana
Abronia villosa
Lupinus arizonicus
Mimulus bigelovii
Eschscholzia californica
Perennials
Eriogonum fasciculatum
Bebbia juncea
Encelia farinosa
Salazaria mexicana
Senna armata
Gutierrezia sarothrae
Sporobolus airoides
Larrea tridentata
Ambrosia dumosa
Hymenoclea salsola
Aristida purpurea
Asclepias subulata
Baileya multiradiata
Pleuraphis rigida
Stephanomeria pauciflora

Fig. 1

Interpretive Summary

Identifying native species, for use in revegetation and plant community augmentation projects, capable of reducing the fitness of invasive species is a major thrust in invasive species science and management. We sought to identify native species competitive with *Bromus rubens*, an exotic annual grass increasing fuel loads and facilitating fires devastating to resources in southwestern USA arid lands. In a greenhouse experiment screening the competitive abilities of 27 native species, we found that the native annuals *Chaenactis stevioides* and *Amsinckia tessellata* and the perennials *Eriogonum fasciculatum*, *Bebbia juncea*, and *Encelia farinosa* mostly strongly competed with *Bromus*. In a companion field assessment of *Bromus* below different native perennial plants in the eastern Mojave Desert, *Bromus* cover varied more than 9-fold among 16 species. Species such as *Thamnosma montana*, *B. juncea*, *E. farinosa*, and *E. fasciculatum* showed promise in their ability to support low levels of *Bromus* cover, whereas *Krameria erecta* seems to facilitate *Bromus*. There is potential to develop lists of species for practitioners to recommend or avoid using in desert revegetation projects based on species' interactions with *Bromus*.