RESEARCH ARTICLE

Identifying Native Vegetation for Reducing Exotic Species during the Restoration of Desert Ecosystems

Scott R. Abella,[1,2] Donovan J. Craig,[1] Stanley D. Smith,[3] and Alice C. Newton[4]

Abstract

There is currently much interest in restoration ecology in identifying native vegetation that can decrease the invasibility by exotic species of environments undergoing restoration. However, uncertainty remains about restoration's ability to limit exotic species, particularly in deserts where facilitative interactions between plants are prevalent. Using candidate native species for restoration in the Mojave Desert of the southwestern U.S.A., we experimentally assembled a range of plant communities from early successional forbs to late-successional shrubs and assessed which vegetation types reduced the establishment of the priority invasive annuals *Bromus rubens* (red brome) and *Schismus* spp. (Mediterranean grass) in control and N-enriched soils. Compared to early successional grass and shrub and late-successional shrub communities, an early forb community best resisted invasion, reducing exotic species biomass by 88% (N added) and 97% (no N added) relative to controls (no native plants). In native species monocultures, *Sphaeralcea ambigua* (desert globemallow), an early successional forb, was the least invasible, reducing exotic biomass by 91%. However, the least-invaded vegetation types did not reduce soil N or P relative to other vegetation types nor was native plant cover linked to invasibility, suggesting that other traits influenced native-exotic species interactions. This study provides experimental field evidence that native vegetation types exist that may reduce exotic grass establishment in the Mojave Desert, and that these candidates for restoration are not necessarily late-successional communities. More generally, results indicate the importance of careful native species selection when exotic species invasions must be constrained for restoration to be successful.

Key words: *Bromus rubens*, competition, invasion-reducing communities, native-exotic species relationships, nitrogen, restoring resistance, *Schismus*, soil.

Introduction

Ecological restoration in many ecosystems must contend with exotic species that thrive in the disturbed environments in which restoration is conducted. A fundamental goal in restoration is promoting ecosystems dominated by native species with minimal amounts of exotic species, which is a property restored ecosystems exhibit for restoration to be considered successful (SER 2004). There is much current interest in establishing vegetation types, sometimes incrementally through time, which can reduce the invasion of exotic species (Bakker and Wilson 2004; Simmons 2005; James et al. 2006). Success has varied, however. In grasslands of Saskatchewan, Canada, for instance, Bakker and Wilson (2004) found that seeding a mixture of native species reduced the frequency of the exotic perennial grass *Agropyron cristatum* (crested wheatgrass) by 33%. In contrast, Thacker et al. (2009) did not find that establishing native species decreased the exotic annual *Bromus tectorum* (cheatgrass) in southwestern U.S.A. arid lands. Owing to the high prevalence of facilitative plant interactions in arid lands, where established plants ameliorate environmental conditions and improve the recruitment of other species (Rodríguez-Buriticá & Miriti 2009), establishing native plants through restoration could be particularly uncertain in arid lands as a strategy for decreasing exotic species invasions.

Theories related to species selection in restoration for the purpose of decreasing community invasibility by exotic species include the "sampling effect" and "limiting similarity." Sampling-effect theory suggests that when considering increasing numbers of resident species, the probability increases of a resident species being present that is a strong competitor with a potential invader and the success of the invader is linked to the presence or absence of one or a few highly competitive resident species (Kennedy et al. 2002). Limiting-similarity theory predicts that the most invasible communities are those that lack resident species that are similar to a potential invader (Emery 2007). For example, the theory suggests that resident communities of grasses would be most resistant to invasion by other grass species.

[1] Department of Environmental and Occupational Health, University of Nevada Las Vegas, Las Vegas, NV 89154-3064, U.S.A.
[2] Address correspondence to S. R. Abella, email scott.abella@unlv.edu
[3] School of Life Sciences, University of Nevada Las Vegas, Las Vegas, NV 89154-4004, U.S.A.
[4] National Park Service, Lake Mead National Recreation Area, 601 Nevada Way, Boulder City, NV 89005, U.S.A.

In addition to resident species composition, soil fertility is one of the major factors predicted to influence invasibility within native communities (Seabloom et al. 2003). Habitats containing high levels of soil nutrients such as N are generally considered to promote establishment of exotic plants, as more resources are available to invaders that often are less conservative in their resource use than natives (DeFalco et al. 2003). Native plant species that can reduce soil nutrient concentrations by acquiring nutrients into their biomass can decrease soil resources available to exotic species (Tilman & Wedin 1991). However, the ability of native vegetation to reduce soil nutrients can vary sharply, making this a source of uncertainty for identifying native species that are restoration candidates potentially able to decrease the establishment of exotic species (James et al. 2008).

Similar to many other ecosystems, widespread invasion of exotic species has complicated restoration in the arid lands of the American West (Sheley et al. 2006; Steers & Allen 2010). Exotic grasses have increased fuel loads in these arid lands, facilitating fire spread in ecosystems that were historically fuel-limited before invasion (D'Antonio & Vitousek 1992). For example, an alarming 3% of the 124,000-km^2 Mojave Desert burned in 2005 alone (Brooks & Matchett 2006). With exotic annual grasses such as *Bromus rubens* (red brome) and *Schismus* spp. (*arabicus* and *barbatus*; Mediterranean grass) firmly established in this region, every moist year when annual plant growth is stimulated has potential to have an active summer fire season once the grass fuel dries and temperatures rise (Rao et al. 2010). Following these fires, the natural reestablishment of native perennial plant cover typically requires 40 years and late-successional species composition several centuries to indeterminate time periods (Abella 2010). In contrast, the exotic grasses often resurge following fire, transforming native shrublands to fire-controlled exotic annual grasslands (D'Antonio & Vitousek 1992). When restoration is attempted on burns or other disturbances, strategies for reducing exotic grasses must be effective or additional fires are probable, further degrading indigenous ecosystems and negating restoration efforts. In addition, anthropogenic N deposition increases fertility of naturally infertile desert soils and has enhanced the establishment of exotic grasses in the Mojave Desert (Brooks 2003; Rao et al. 2010). Thus, identifying native species for restoration should consider whether these species will be effective at limiting exotic species on N-enriched soils.

We evaluated the abilities of candidate native species for restoration to reduce the establishment of exotic species in soils with and without N addition. We conducted the study in the Mojave Desert using native species varying in growth form and successional status to represent a range of species for consideration for restoration and focused on the most problematic invasive grasses: *B. rubens* (hereafter *Bromus*) and *Schismus* spp. (hereafter *Schismus*). We hypothesized that native vegetation types would vary in their abilities to limit exotic grass establishment and those that reduced soil N would be most effective. More specifically, based on the sampling-effect theory, we anticipated that only a small subset of native species within communities would reduce exotic

species invasion success. Moreover, based on the limiting-similarity theory, we expected that native species with growth forms (i.e. grasses) most similar to the exotic species would best resist invasion.

Methods

This study occurred outside and adjacent to the experimental plant nursery within Lake Mead National Recreation Area (LMNRA), in the eastern Mojave Desert, 16 km east of Las Vegas, Nevada, southwestern U.S.A. (36°03′30′N, 114°49′26′W, 381 m in elevation). Surrounding vegetation was Mojave Desert scrub, dominated by *Larrea tridentata* (creosote bush) and *Ambrosia dumosa* (white bursage). For the study, the previously disturbed site was graded using heavy equipment and an area of 0.05 ha was created for community plots and 0.01 ha for species plots. An enclosure, 1.25 m tall with mesh openings 0.6 cm in diameter and aluminum flashing to a height of 45 cm, was installed around the entire site to deter vertebrate herbivory. Community plots, 2 m × 2 m in area, were spaced 0.5 m apart, and 1 m × 1 m species plots were also spaced in rows 0.5 m apart. Soil within plots was excavated to a depth of 0.25 m and replaced with a commercially available sandy loam mixture typical of desert soils (Boulder Sand and Gravel Co., Boulder City, NV, U.S.A.). These plot soils averaged 76 ± 3% sand (mean ± SD), 12 ± 2% silt, and 12 ± 2% clay (hydrometer method; Burt 2004). A strip of aluminum flashing, 45 cm tall, was installed 20 cm deep into the soil around each plot to further discourage herbivory and reduce interaction between plots.

The community experiment was a three-way factorial design consisting of native plant community (five levels: early successional forb, shrub, and grass; late-successional shrub; or control with no native plants), exotic species (two levels: *Bromus* or *Schismus* added to plots), and N addition (two levels: added or not), with each of the 20 treatment combinations replicated three times. Three species (all perennial) constituted each of the native plant communities as follows: early forb—*Baileya multiradiata* (desert marigold), *Penstemon bicolor* (pinto beardtongue), and *Sphaeralcea ambigua* (desert globemallow); early grass—*Achnatherum hymenoides* (Indian ricegrass), *Aristida purpurea* (purple threeawn), and *Sporobolus airoides* (alkali sacaton); early shrub—*Bebbia juncea* (sweetbush), *Encelia farinosa* (brittlebush), and *Hymenoclea salsola* (cheesebush); and late shrub—*A. dumosa*, *Eriogonum fasciculatum* (eastern Mojave buckwheat), and *L. tridentata* (nomenclature and growth-form classification follow NRCS (2011)). The successional classification of species was based on data from 47 studies in the Mojave and Sonoran Deserts using a ratio of disturbed:undisturbed abundance among studies (Abella 2010).

The species experiment was a two-way, factorial design including 13 levels of native species (the 12 species from the community experiment each in their own plot and a control with no native vegetation) and two levels of exotic species addition (*Bromus* or *Schismus*), with each of the 26 treatment

combinations replicated three times. Treatments were assigned to plots in a completely random design in both experiments.

Native species were grown in 1- or 4-L pots in local greenhouses (LMNRA nursery and the College of Southern Nevada, Henderson, NV, U.S.A.) from Mojave Desert seed sources for one year before outplanting. In each community plot receiving the native vegetation treatment, 12 individuals of each of the three assigned native species were randomly planted in a 6×6 array where one individual of each species was present in each set of three plants. This resulted in a density of 3 plants/m^2 for each species and a total of 9 plants/m^2. In species plots, nine individuals of the assigned species were planted in a 3×3 array, also for a density of 9 plants/m^2. In control plots in both experiments, holes were dug and re-filled so that any disturbance associated with planting was constant across all treatment combinations. Native plants were outplanted in plots in December 2008.

Following planting, plots were watered with 0.2 cm/week of tap water from hoses at the nursery facility. We conducted watering to help ensure that the native outplants survived, which is a realistic context for arid land restoration, and also watered control plots so that watering was constant across treatment combinations. A total of 17 cm (83% of average) of natural precipitation fell at the site during the 16-month study period from January 2009 through April 2010. The 73-year average is 14 cm/year based on the Boulder City, Nevada weather station 10 km away (Western Regional Climate Center, Reno, NV, U.S.A.). Seeds of either *Bromus* or *Schismus* were seeded at a density of 100 seeds/m^2 to appropriate plots in both experiments during February 2009 to establish an initial seed bank. Seeds were collected within LMNRA and had a germinability of 50% in pots with soil in greenhouse conditions (daily watering and constant $24°C$ temperature). A second seeding, using a higher density of 700 seeds/m^2 to provide a propagule pressure that could result in ≥ 50 plants/m^2 (the initial seeding of 100 seeds/plot produced 8 plants/m^2), was done in September 2009. Initial applications of N in community plots were performed in February and March 2009, followed by applications in December 2009 and February 2010. Nitrogen was added as NH_4-NO_3 at a rate of 1.7 g N/m^2 to plots in each of the four applications. This resulted in 3.4 g/m^2/yr of N for each growing year, similar to Brooks' (2003) 3.2 g/m^2/yr in a previous N addition experiment in the Mojave Desert.

Data were collected after the second spring, in May 2010, at the time of peak biomass of annual plants. Aboveground biomass of exotic grasses was harvested from plots and weighed following oven drying at $60°C$ for 72 hours. Aerial cover of native plants was categorized using 5% cover classes. Samples of the 0–5 cm soil layer were collected from centers of plots, sieved to 2 mm, and analyzed for NH_4-N (2 M KCl extraction, salicylate method), NO_3-N (2 M KCl extraction, ion chromatography method), total C and N (dry combustion), organic C (difference between total C and inorganic C), and available P (Olsen method) following Burt (2004). Samples were immediately placed in a chilled cooler and analyzed within 24 hours for NH_4 and NO_3. Foliar samples of native

and exotic species were collected from community plots and of native species on species plots (samples of the exotics were collected on controls), ground with a stainless-steel blender, digested with a sulfuric acid–hydrogen peroxide procedure, and analyzed colorimetrically for N and P (Allen 1989).

Response variables of exotic species biomass (transformed as square root) and soil and foliar nutrients were analyzed for both experiments using analysis of variance including all possible factorial interactions with Tukey's test for multiple comparisons in JMP software (SAS Institute 2004). The relationship between cover of native species and biomass of exotic species was assessed using Pearson and Spearman correlation coefficients.

Results

Community Experiment

Two-way interactions between native plant community type and both exotic species identity and N addition, and between exotic species and N addition, were significant in influencing the biomass of the exotic species, *Bromus* and *Schismus* (Table 1). In the native community $\times$ exotic species interaction, *Bromus* had 5- to 13-fold greater biomass in the early successional grass community and control (no native vegetation) than did *Schismus* (Fig. 1a). *Bromus* produced significantly greater biomass in the control and grass communities than in the early and late shrub and early forb communities, with the forb community averaging one-third lower *Bromus* biomass than any other community. In the community $\times$ N interaction, the forb community was the only one to support significantly lower exotic species biomass than controls both with and without N addition (Fig. 1b). In the absence of N addition, the late-successional shrub community harbored significantly lower exotic biomass than the control. *Bromus* had significantly greater biomass with N addition than without, and significantly greater biomass than *Schismus* in the respective N treatments in the exotic species $\times$ N interaction (Fig. 1c). The correlation between native species cover and exotic biomass was -0.40 ($p < 0.01$) for both Pearson and Spearman's r.

There were no significant interactions for any of the soil or foliar nutrients, but there were significant main effects of community type on soil NH_4-N, P, organic C, and exotic and native foliar N; of exotic species on foliar P; and of N addition on all soil and foliar N variables (Table 1). Nitrogen addition increased soil NH_4-N by 6-fold over no N, doubled soil NO_3-N, and increased foliar N in the exotic species by 50% and in native species by 15% (Table S1). In community type effects, the control and forb communities exhibited 2- to 3-fold greater soil NH_4-N than the other communities. In contrast, for soil P, the early shrub community had significantly greater concentrations (1.5- to 3-fold) than the forb, late shrub, and control communities. Similarly, the early shrub community exhibited 2-fold greater soil organic C than the next highest communities (forb and grass) and 5-fold greater than the control. Considering the concentration of N in foliage of exotic grasses, the control averaged twice as much foliar

Table 1. Analysis of variance results for the influences of native plant community type, identity of exotic species, and nitrogen addition on the biomass of exotic grasses, soil nutrients, and foliar nutrients in experimental communities in the Mojave Desert, U.S.A.

	Effect							
	Community (C)[b]	*Exotic (E)*	*Nitrogen (N)*	*C × E*	*C × N*	*E × N*	*C × E × N*	*Model*[c]
Response Variable[a]	*F-statistic (probability)*							*r²*
Exotic biomass	**13.6 (<0.001)**	**69.9 (<0.001)**	**32.4 (<0.001)**	**5.8 (<0.001)**	**3.4 (0.018)**	**5.1 (0.030)**	1.2 (0.327)	0.84
Soil NH_4-N	**3.3 (0.021)**	0.1 (0.770)	**23.5 (<0.001)**	2.2 (0.081)	1.7 (0.174)	0.1 (0.815)	1.9 (0.127)	0.60
Soil NO_3-N	0.7 (0.620)	0.4 (0.537)	**30.5 (<0.001)**	1.2 (0.343)	0.1 (0.976)	0.2 (0.643)	0.8 (0.546)	0.52
Soil total N	2.5 (0.056)	0.3 (0.568)	0.7 (0.401)	0.3 (0.858)	0.9 (0.456)	0.7 (0.404)	0.4 (0.815)	0.32
Soil P	**9.9 (<0.001)**	0.4 (0.542)	0.0 (0.936)	0.7 (0.603)	0.0 (0.998)	1.2 (0.287)	0.4 (0.838)	0.53
Soil organic C	**5.2 (0.002)**	0.6 (0.440)	0.0 (0.851)	0.3 (0.891)	0.7 (0.598)	1.3 (0.269)	0.2 (0.913)	0.41
Exotic foliar N	**2.9 (0.034)**	0.0 (0.936)	**7.3 (0.010)**	1.6 (0.182)	0.4 (0.825)	0.0 (0.827)	1.2 (0.314)	0.47
Exotic foliar P	0.4 (0.775)	**5.4 (0.026)**	3.2 (0.081)	0.3 (0.867)	0.8 (0.505)	0.0 (0.981)	0.6 (0.691)	0.31
Native foliar N	**15.5 (<0.001)**	0.1 (0.800)	**6.5 (0.016)**	0.9 (0.442)	0.3 (0.813)	0.0 (0.942)	0.1 (0.952)	0.42
Native foliar P	2.3 (0.092)	0.2 (0.700)	0.2 (0.698)	1.3 (0.278)	0.7 (0.570)	0.6 (0.426)	1.2 (0.317)	0.27

[a] Degrees of freedom for all variables except for native foliar N and P (in order of effects): 4, 1, 1, 4, 4, 1, 4. For native foliar N and P: 3, 1, 1, 3, 3, 1, 3. The measurement unit for exotic biomass (consisting of *Bromus rubens* and *Schismus* spp.) is g/m² and the unit for soil and foliar variables is concentration by weight (μg/g or %).
[b] Native community types are represented by early successional forb, grass, and shrub; late-succesional shrub; and control (no native vegetation).
[c] Overall model r^2.

N as the lowest community (early shrub), with the other communities exhibiting values similar to the control. The early and late shrub communities contained significantly greater native species foliar N than the forb and grass communities. In the only main effect of exotic species identity on soil or foliar nutrients, *Schismus* had greater foliar P than *Bromus*.

Species Experiment

As in the community experiment, the only significant interaction was for exotic species biomass, where identity of the native interacted with identity of the exotic species (Table 2). This interaction resulted from *Bromus* exhibiting greater biomass than *Schismus* in 7 of 13 (54%) native species treatments. In addition, the early successional forb *Sphaeralcea ambigua* was the only species supporting significantly lower *Bromus* biomass than the control. Cover of native species had Pearson and Spearman *r*'s of −0.20 (*p* = 0.08) with exotic species biomass (Fig. 2).

For main effects on soil and foliar nutrients, *Encelia farinosa* and *Bebbia juncea* had greater soil total N than the control, *Penstemon bicolor*, *Ambrosia dumosa*, *Larrea tridentata*, and *Sporobolus airoides* (Tables 2 and S2). Results were similar but more pronounced for soil P, where *Bebbia* and *Encelia* exhibited the highest concentrations, and also similar for soil organic C where *Bebbia* was significantly greater than the control and five of the species including *Larrea* and *Ambrosia*. *Hymenoclea salsola* and *Ambrosia* had significantly greater foliar N than the control and *Penstemon*, *Achnatherum hymenoides*, and *Aristida purpurea*. In the only effect of exotic species identity, *Bromus* had 15% greater foliar N than *Schismus*.

Discussion

We found that different native vegetation types varied sharply in their ability to reduce exotic species establishment. Results supported the sampling-effect theory (Kennedy et al. 2002) in that a limited number of species (e.g. *Sphaeralcea ambigua*) were most effective at resisting invasion from among the pool of 12 native species that were evaluated. This suggests that efforts that screen a large number of native species for restoration have potential to reveal additional species that are effective. Conversely, the limiting-similarity theory (Emery 2007) was not supported, as the native species most similar in growth form (the grasses) to the exotic species were not the most competitive. However, it cannot be dismissed that similarity in traits other than growth form may have influenced competitive interactions.

Results highlighted the importance of species selection as a key part of restoration for controlling exotic species. In particular, the early successional forb community (apparently largely driven by *S. ambigua*) was the only community to significantly reduce exotic species biomass in both control and N-enriched soils. Conversely, the early successional perennial grass community did not reduce invasibility, and the early shrub community performed similarly to the late shrub community. Species within our experimental community types displayed variation in the species monoculture plots, suggesting the potential for combining species by growth forms in different ways for maximizing community resistance to invasion. For example, grouping the best-performing species from each community (e.g. *S. ambigua* from the early forb, *Sporobolus airoides* early grass, and *Encelia farinosa* early shrub) at a given level of species richness would appear to most effectively decrease community invasibility. However, the greater variety of resident growth forms could promote invasibility by creating more microsites and potential facilitative effects for invaders (Levine et al. 2004). Moreover, invasibility may change through time as succession proceeds and the native communities themselves are likely to change. These observations highlight the need for further research that examines the effectiveness of different species combinations and minimum
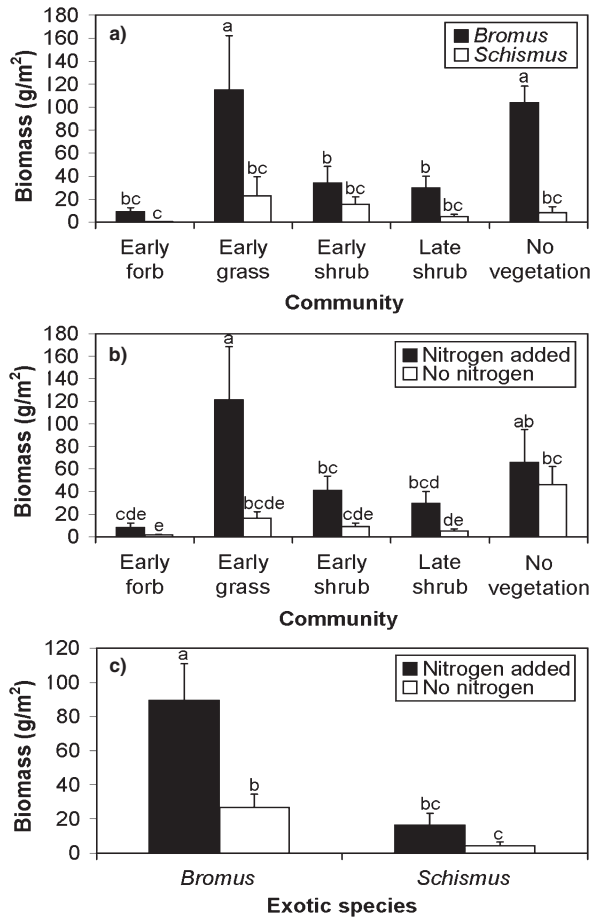
Figure 1. Responses of exotic species biomass to the experimental factors of constructed native community type and N addition in the Mojave Desert, U.S.A. (a) Native community type × exotic species (*Bromus rubens* or *Schismus* spp.); (b) native community type × soil N addition; (c) exotic species × N addition. Error bars are standard errors of the means. Means without shared letters within an interaction differ at $p < 0.05$ (Tukey's test).
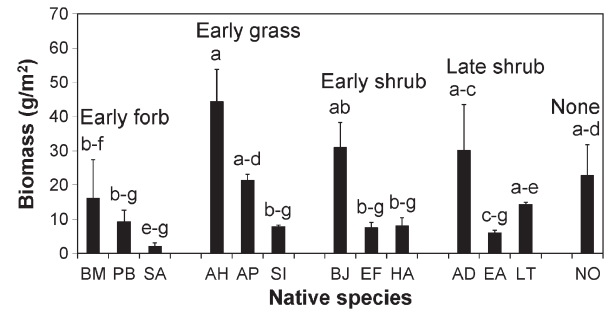

Figure 2. Effects of native perennial species on the biomass of the exotic annual *Bromus rubens* in the Mojave Desert, U.S.A. Error bars are standard errors of the means. Means without shared letters differ at $p < 0.05$ (Tukey's test). Native species are organized by successional stage (e.g. early forb) and are abbreviated as: BM, *Baileya multiradiata*; PB, *Penstemon bicolor*; SA, *Sphaeralcea ambigua*; AH, *Achnatherum hymenoides*; AP, *Aristida purpurea*; SI, *Sporobolus airoides*; BJ, *Bebbia juncea*; EF, *Encelia farinosa*; HS, *Hymenoclea salsola*; AD, *Ambrosia dumosa*; EA, *Eriogonum fasciculatum*; LT, *Larrea tridentata*; and NO, none (control, no native vegetation). Because the biomass of the second exotic annual, *Schismus* spp., was minimal, only *Bromus* is shown. In multiple comparisons for the full native species × exotic species interaction, *Schismus* mean biomass has the letter 'g' for all native species except for AH ('d-g') and BJ ('fg') for comparison to *Bromus* biomass shown in this figure across native species.

Table 2. Analysis of variance results for the influences of native species and identity of exotic species on the biomass of exotic grasses, soil nutrients, and foliar nutrients in experimental communities in the Mojave Desert, U.S.A.

Response Variable[a]	Native Species (NS)[b]	Exotic Species (ES)	NS × ES	Model[c]
	F-statistic (probability)			r^2
Exotic biomass	**5.5 (<0.001)**	**259.0 (<0.001)**	**2.4 (0.017)**	0.87
Soil NH$_4$-N	1.6 (0.108)	0.0 (0.944)	0.9 (0.510)	0.37
Soil NO$_3$-N	0.6 (0.811)	1.1 (0.296)	0.7 (0.769)	0.24
Soil total N	**4.3 (<0.001)**	0.6 (0.432)	1.7 (0.106)	0.58
Soil P	**7.5 (<0.001)**	0.2 (0.673)	1.5 (0.150)	0.68
Soil organic C	**4.2 (<0.001)**	0.5 (0.494)	1.0 (0.468)	0.55
Foliar N	**4.8 (<0.001)**	**4.8 (0.034)**	0.8 (0.605)	0.59
Foliar P	0.7 (0.707)	0.3 (0.604)	0.8 (0.651)	0.27

[a] Degrees of freedom for all variables (in order of effects): 12, 1, 12. The measurement unit for exotic biomass (consisting of *Bromus rubens* and *Schismus* spp.) is g/m^2 and the unit for soil and foliar variables is concentration by weight (µg/g or %).
[b] Included a control (no native vegetation) and 12 native species grown in single-species plots ranging from early successional forbs such as *Sphaeralcea ambigua* to late-succesional shrubs such as *Larrea tridentata*.
[c] Overall model r^2.

densities required for each native vegetation type for achieving reductions in exotic species through time.

Nitrogen addition influenced exotic species establishment across communities, but in contrast to the a priori expectation, the least-invaded native vegetation types did not reduce soil N or P to the lowest levels. Nitrogen addition in control and early grass communities boosted exotic grass biomass production to be near or exceed a 100 g/m^2 threshold estimated for fire spread in the Mojave Desert (Rao et al. 2010). However, while N addition promoted exotic biomass in all native communities, invasibility of the early forb community was the least affected by N addition. Given that our amount of N addition (3.4 g/m^2/yr for each growing year) exceeds current rates of N deposition (e.g. 0.3–0.8 [Rao et al. 2010] and 3.2 g/m^2/yr [Brooks 2003]) reported in the Mojave Desert, the early forb community may reduce invasibility even if anthropogenic N deposition increases. Manipulating other resources, such as water, would be useful in future experiments to evaluate if acquisitions of resources other than soil nutrients or if other traits (e.g. allelopathy) of native species more strongly impact invasion resistance (James et al. 2008).

Isolating traits of native species that would result in being most strongly competitive with exotic C$_3$ grasses remains elusive. In moist years supporting annual plants, exotic grasses germinate in fall/winter and vigorously grow and produce seed in March–April when temperatures warm (Beatley 1974).

Species that have periods of active growth most closely corresponding are generally considered to have the greatest potential for competition between them (Tilman & Wedin 1991). However, simple correspondence of native and exotic C₃ species does not exist in the Mojave Desert, where an offset of only a month in the timing of active growth between native species within a photosynthetic pathway can affect competitive relationships with exotic grasses (James et al. 2006). Vigorous growth periods of the native species used in our experiments partially overlap with those of the exotic grasses in spring (March–April; Beatley 1974), but as Corbin and D'Antonio (2004) noted, occupancy of space or other interference can affect species relationships even if growth periods of the species do not completely overlap. We did not include grazing in our experiment, and susceptibility to grazing could be a trait influencing competitive interactions. A review (Abella 2008) of grazing effects in the Mojave Desert suggested that the most preferentially grazed plant group is perennial grasses, which performed poorly in our experiment even when protected from grazing. However, especially in drier years many plant groups (even non-preferred species) can be eaten by a variety of herbivores, suggesting that the potential influence of herbivory should be included when selecting native plants for restoration.

Plant size and tendency to concentrate nutrients by forming fertile islands are additional traits that could influence the competitive abilities of native species with exotic annuals. We did not find a strong relationship of native plant cover with exotic biomass in the short term. This finding is consistent, however, with a non-manipulative field study in older, mature plant communities in the Mojave Desert that reported no relationship between native plant size and the cover of *Bromus* (Abella et al. 2011). While plant size often determines competitive ability in more mesic ecosystems, other traits such as canopy architecture, timing of germination, and soil modification related to fertile islands (resulting in facilitation rather than competition) may be more important in deserts. Interestingly, the species that best reduced invasion were those (e.g. *S. ambigua* and *E. farinosa*) that do not form well-established fertile islands (Abella 2010).

One factor that is unique to this region from a restoration perspective is desert scrub structure of vegetation, with <20% perennial cover on many sites (Smith et al. 1997). In this vegetation type, exotic grasses readily establish in open interspaces in addition to exploiting high-N microsites beneath shrubs. Therefore, earlier successional communities that potentially create a higher, less patchy cover may indeed be more effective in limiting exotic species establishment through competitive effects, whereas late-successional scrub communities provide little competitive effect in interspaces (a majority of the space) and facilitative effects within fertile islands beneath shrubs (Rodríguez-Buriticá & Miriti 2009).

To be the most useful for restoration, the species that best limited exotic grasses should also be amenable to establishment through seeding or planting. On the basis of a review of published revegetation studies in the Mojave Desert (Abella & Newton 2009), some of the early forb species examined in this study have become established in one or more seeding studies.

Baileya multiradiata and *Penstemon bicolor* both became established in the one study each in which they were examined, while *S. ambigua* did not become established. However, *S. ambigua* did become established during the first year of a post-fire seeding in the Sonoran Desert (Abella et al. 2009). We suggest further seeding and planting trials with this species, as well as techniques that could augment its observed natural initial colonization of disturbances (Abella 2010). Some of the other species in monoculture plots not among those most heavily invaded by *Bromus*, including *Hymenoclea salsola*, *S. airoides*, and *Eriogonum fasciculatum*, have become established in one or more studies through planting or seeding (Abella & Newton 2009).

A main finding of this study was that some native communities and species monocultures reduced the biomass of exotic annual grasses relative to controls (no native vegetation) to levels far below the Mojave Desert "fire threshold" (Rao et al. 2010). This finding is unique, as most previous research with exotic grasses in southwestern arid lands has focused on the one-way interactions of effects of the exotics on natives (and not effects of natives on the exotics) or have found that native species facilitate exotic species establishment (DeFalco et al. 2003; Rodríguez-Buriticá & Miriti 2009). Furthermore, our results suggest that earlier successional communities may be more effective than later mature communities in limiting the establishment of exotic grasses, and testing additional native species for this ability including over longer time periods is warranted. Through careful species selection, results suggest that there is potential for identifying native communities that can reduce invasibility when constraining ecosystem-transforming exotic species is a key to restoration success.

Implications for Practice

- Invasions by exotic species can undermine restoration efforts. In arid lands of the North American Southwest, native species that can both become established and compete with exotic annual grasses are needed for restoration in disturbed habitats following wildfires.
- At a Mojave Desert field site, we found that early successional forb vegetation reduced biomass of two exotic annual grasses (red brome and Mediterranean grass) relative to controls (not containing native vegetation) in both control and N-enriched soils. Desert globemallow was particularly effective and is a recommended species for restoration.
- This study highlights that matching growth forms of native to exotic invasive species (e.g. grass:grass) is not necessarily the best method for identifying native species that may compete successfully with invasive species during restoration projects. In deserts, traits of native species such as the extent of fertile island formation may be more closely related to interactions between native and exotic species than traits such as plant size or similarity in growth forms.

Acknowledgments

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Means of exotic grass biomass and soil and foliar nutrients by treatment for the community experiment.
Table S2. Means of exotic grass biomass and soil and foliar nutrients by treatment for the species experiment.

Appendix S1. Means and standard errors of means in the community experiment for response variables by the treatment factors of experimental plant community type, nitrogen addition, and exotic annual grass introduced (*Bromus rubens* or *Schismus* spp.) at an experimental site in the eastern Mojave Desert, U.S.A.

						Soil				Foliar			
Treatments			Biomass	NH_4-N	NO_3-N	Total N	P	Organic C	Exotic N	Exotic P	Native N	Native P
Community	N added	Exotic	g/m^2	µg/g	µg/g	%	µg/g	%	%	%	%	%
Early forb	No	*Bromus*	2.7±0.8	1.8±0.9	2.7±0.4	0.011±0.003	29.6±15.5	0.08±0.03	0.8±0.3	0.15±0.04	1.8±0.3	0.14±0.01
	No	*Schismus*	0.1±0.1	0.6±0.4	2.8±0.6	0.014±0.003	52.5±01.5	0.25±0.06	0.6±0.1	0.27±0.22	2.1±0.3	0.11±0.01
	Yes	*Bromus*	15.5±5.1	13.0±8.6	8.8±4.1	0.018±0.005	37.3±18.3	0.27±0.14	0.9±0.5	0.07±0.03	2.2±0.1	0.17±0.06
	Yes	*Schismus*	0.8±0.2	6.5±1.0	4.6±1.0	0.021±0.005	51.6±07.8	0.43±0.17	1.4±0.3	0.16±0.01	2.2±0.1	0.13±0.02
Early grass	No	*Bromus*	29.1±1.4	0.5±0.1	2.8±0.4	0.014±0.004	51.2±16.7	0.31±0.14	0.3±0.1	0.12±0.03	1.6±0.2	0.08±0.01
	No	*Schismus*	4.2±1.8	0.9±0.7	2.7±0.3	0.016±0.008	43.9±10.8	0.21±0.14	0.8±0.2	0.20±0.07	1.2±0.1	0.14±0.03
	Yes	*Bromus*	200.8±62.0	4.2±2.4	4.7±0.7	0.013±0.005	47.8±11.6	0.20±0.12	0.8±0.4	0.11±0.01	2.0±0.2	0.11±0.02
	Yes	*Schismus*	41.4±32.2	3.1±0.6	6.2±0.5	0.021±0.007	49.6±08.8	0.31±0.21	0.6±0.2	0.12±0.04	1.8±0.1	0.13±0.03
Early shrub	No	*Bromus*	15.2±2.5	0.7±0.4	2.1±0.2	0.026±0.003	68.4±05.5	0.72±0.29	0.4±0.2	0.17±0.06	2.4±0.1	0.16±0.05
	No	*Schismus*	2.6±1.2	0.8±0.2	2.3±0.2	0.023±0.008	63.0±06.2	0.52±0.18	0.5±0.0	0.19±0.05	2.6±0.2	0.16±0.05
	Yes	*Bromus*	52.7±25.9	5.7±1.5	5.9±0.2	0.022±0.006	64.6±13.1	0.44±0.27	0.8±0.4	0.13±0.08	2.6±0.1	0.12±0.01
	Yes	*Schismus*	28.5±5.9	2.3±0.7	5.2±0.9	0.020±0.002	66.3±04.5	0.58±0.23	0.6±0.1	0.25±0.09	2.8±0.4	0.14±0.04
Late shrub	No	*Bromus*	8.8±1.5	0.1±0.1	2.0±0.0	0.013±0.007	35.7±10.4	0.23±0.09	0.2±0.0	0.21±0.05	2.5±0.3	0.23±0.04
	No	*Schismus*	1.2±0.3	1.3±0.9	2.5±0.2	0.012±0.002	25.7±04.5	0.25±0.08	0.6±0.1	0.2±0.030	2.6±0.2	0.14±0.00
	Yes	*Bromus*	50.0±11.4	2.2±1.0	4.9±0.8	0.011±0.003	22.4±11.8	0.13±0.10	0.9±0.3	0.08±0.02	2.8±0.5	0.15±0.01
	Yes	*Schismus*	8.5±2.8	4.5±0.7	7.1±1.9	0.009±0.001	35.2±09.8	0.16±0.05	0.9±0.2	0.14±0.03	2.8±0.1	0.17±0.04
No natives	No	*Bromus*	78.3±13.1	2.4±1.8	4.1±1.9	0.011±0.002	28.3±06.5	0.07±0.02	1.3±0.3	0.13±0.04	—	—
	No	*Schismus*	13.5±10.6	2.2±1.5	2.9±0.1	0.006±0.003	16.9±03.5	0.06±0.03	0.6±0.3	0.21±0.04	—	—
	Yes	*Bromus*	128.9±16.0	5.4±0.8	8.1±2.9	0.011±0.001	17.1±00.4	0.05±0.01	1.3±0.2	0.17±0.03	—	—
	Yes	*Schismus*	2.9±0.9	16.8±4.7	5.8±1.1	0.022±0.016	27.1±19.0	0.26±0.19	1.0±0.2	0.18±0.06	—	—

Appendix S2. Means and standard errors of means in the species experiment for response variables by the treatment factors of native species (organized by successional classification) and exotic annual grass introduced (*Bromus rubens* or *Schismus* spp.) at an experimental site in the eastern Mojave Desert, U.S.A. Biomass represents the biomass of the exotic grasses (either *Bromus* or *Schismus*). Foliar data are for the native species except in the control not containing native vegetation, where foliar values represent either *Bromus* or *Schismus*.

Community	Exotic	Biomass g/m^2	NH$_4$-N µg/g	NO$_3$-N µg/g	Soil Total N %	Soil P µg/g	Soil Organic C %	Foliar N %	Foliar P %
Early forb									
Baileya multiradiata	***Bromus***	**16.0±11.4**	**0.5±0.2**	**4.8±1.6**	**0.008±0.002**	**15.1±10.2**	**0.05±0.02**	**1.8±0.2**	**0.11±0.03**
	Schismus	0.0±0.0	2.4±0.3	2.8±0.4	0.011±0.001	30.5±12.9	0.10±0.02	1.9±0.3	0.13±0.01
Penstemon bicolor	***Bromus***	**9.2±3.5**	**1.0±0.5**	**5.1±1.9**	**0.009±0.003**	**12.3±5.7**	**0.12±0.07**	**1.6±0.3**	**0.10±0.01**
	Schismus	0.0±0.0	1.9±0.5	2.5±0.7	0.005±0.001	10.5±3.5	0.06±0.01	1.0±0.1	0.09±0.04
Sphaeralcea ambigua	***Bromus***	**2.1±1.0**	**2.3±0.6**	**3.3±0.6**	**0.010±0.001**	**30.5±2.5**	**0.13±0.01**	**1.9±0.2**	**0.11±0.01**
	Schismus	0.0±0.0	3.2±1.1	2.1±0.7	0.020±0.006	62.4±10.5	0.21±0.11	1.8±0.1	0.14±0.02
Early grass									
Achnatherum hymenoides	***Bromus***	**44.3±9.5**	**1.4±0.6**	**2.4±0.2**	**0.013±0.004**	**42.5±17.8**	**0.13±0.03**	**1.5±0.3**	**0.14±0.04**
	Schismus	4.4±3.5	1.1±0.4	3.0±0.2	0.016±0.008	46.9±26.9	0.13±0.11	1.1±0.2	0.11±0.03
Aristida purpurea	***Bromus***	**21.3±1.8**	**1.2±0.6**	**5.3±2.7**	**0.011±0.001**	**42.4±6.6**	**0.09±0.02**	**1.1±0.1**	**0.12±0.02**
	Schismus	0.1±0.1	0.8±0.6	3.7±0.7	0.006±0.001	21.3±2.5	0.04±0.01	1.1±0.1	0.12±0.02
Sporobolus airoides	***Bromus***	**7.9±0.5**	**1.2±0.8**	**2.8±1.9**	**0.008±0.001**	**9.0±1.1**	**0.03±0.02**	**1.8±0.5**	**0.11±0.02**
	Schismus	0.0±0.0	1.0±0.3	4.3±1.2	0.004±0.001	7.0±2.7	0.05±0.01	1.3±0.2	0.09±0.01
Early shrub									
Bebbia juncea	***Bromus***	**30.9±7.3**	**1.6±0.2**	**2.9±0.5**	**0.026±0.006**	**89.0±13.5**	**0.34±0.09**	**2.2±0.4**	**0.11±0.01**
	Schismus	0.6±0.3	1.3±0.3	2.6±0.1	0.013±0.000	45.2±4.1	0.20±0.07	1.8±0.0	0.15±0.04
Encelia farinosa	***Bromus***	**7.6±1.5**	**2.3±0.5**	**2.3±0.4**	**0.021±0.004**	**60.8±13.9**	**0.24±0.07**	**2.7±0.4**	**0.11±0.02**
	Schismus	0.0±0.0	1.8±0.7	3.5±0.9	0.019±0.008	57.3±24.0	0.21±0.09	2.0±0.2	0.12±0.01
Hymenoclea salsola	***Bromus***	**8.1±2.4**	**1.6±0.7**	**4.3±1.1**	**0.016±0.005**	**48.3±21.2**	**0.21±0.06**	**2.6±0.3**	**0.11±0.01**
	Schismus	0.1±0.1	2.3±0.7	3.2±0.9	0.007±0.001	26.6±8.3	0.06±0.01	2.4±0.1	0.13±0.01

Late shrub								
Ambrosia dumosa	***Bromus***	**30.1±13.4**	**3.3±1.8**	**3.8±0.9**	**0.007±0.001**	**5.7±1.6**	**0.03±0.01**	**2.9±0.6**	**0.14±0.00**
	Schismus	0.0±0.0	1.8±0.3	2.9±0.3	0.006±0.001	6.3±2.1	0.02±0.01	2.2±0.2	0.14±0.03
Eriogonum fasciculatum	***Bromus***	**6.0±0.8**	**1.3±0.5**	**4.2±1.3**	**0.008±0.002**	**5.9±1.5**	**0.09±0.04**	**2.3±0.3**	**0.15±0.03**
	Schismus	0.4±0.4	0.7±0.2	4.0±1.1	0.014±0.003	19.9±5.0	0.19±0.07	1.7±0.2	0.08±0.01
Larrea tridentata	***Bromus***	**14.3±0.6**	**1.5±0.4**	**2.9±0.4**	**0.005±0.000**	**5.3±2.2**	**0.02±0.01**	**1.7±0.3**	**0.17±0.01**
	Schismus	0.1±0.0	1.7±0.9	3.6±0.9	0.008±0.001	11.3±4.9	0.04±0.02	2.2±0.0	0.13±0.01
Control								
No natives	***Bromus***	**22.7±9.1**	**1.2±0.6**	**4.1±0.9**	**0.008±0.002**	**10.2±2.3**	**0.06±0.05**	**1.3±0.3**	**0.13±0.04**
	Schismus	0.4±0.4	0.7±0.4	4.4±1.4	0.006±0.001	8.4±2.8	0.03±0.01	1.4±0.8	0.12±0.04