

Effects of increased soil nitrogen on the dominance of alien annual plants in the Mojave Desert

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Summary

1. Deserts are one of the least invaded ecosystems by plants, possibly due to naturally low levels of soil nitrogen. Increased levels of soil nitrogen caused by atmospheric nitrogen deposition may increase the dominance of invasive alien plants and decrease the diversity of plant communities in desert regions, as it has in other ecosystems. Deserts should be particularly susceptible to even small increases in soil nitrogen levels because the ratio of increased nitrogen to plant biomass is higher compared with most other ecosystems.

2. The hypothesis that increased soil nitrogen will lead to increased dominance by alien plants and decreased plant species diversity was tested in field experiments using nitrogen additions at three sites in the in the Mojave Desert of western North America.

3. Responses of alien and native annual plants to soil nitrogen additions were measured in terms of density, biomass and species richness. Effects of nitrogen additions were evaluated during 2 years of contrasting rainfall and annual plant productivity. The rate of nitrogen addition was similar to published rates of atmospheric nitrogen deposition in urban areas adjacent to the Mojave Desert ($3.2 \text{ g N m}^{-2} \text{ year}^{-1}$). The dominant alien species included the grasses *Bromus madritensis* ssp. *rubens* and *Schismus* spp. (*S. arabicus* and *S. barbatus*) and the forb *Erodium cicutarium*.

4. Soil nitrogen addition increased the density and biomass of alien annual plants during both years, but decreased density, biomass and species richness of native species only during the year of highest annual plant productivity. The negative response of natives may have been due to increased competitive stress for soil water and other nutrients caused by the increased productivity of aliens.

5. The effects of nitrogen additions were significant at both ends of a natural nutrient gradient, beneath creosote bush *Larrea tridentata* canopies and in the interspaces between them, although responses varied among individual alien species. The positive effects of nitrogen addition were highest in the beneath-canopy for *B. rubens* and in interspaces for *Schismus* spp. and *E. cicutarium*.

6. The results indicated that increased levels of soil nitrogen from atmospheric nitrogen deposition or from other sources could increase the dominance of alien annual plants and possibly promote the invasion of new species in desert regions. Increased dominance by alien annuals may decrease the diversity of native annual plants, and increased biomass of alien annual grasses may also increase the frequency of fire.

7. Although nitrogen deposition cannot be controlled by local land managers, the managers need to understand its potential effects on plant communities and ecosystem properties, in particular how these effects may interact with land-use activities that can be managed at the local scale. These interactions are currently unknown, and hinder the ability of managers to make appropriate land-use decisions related to nitrogen deposition in desert ecosystems.

8. *Synthesis and applications.* The effects of nitrogen deposition on invasive alien plants should be considered when deciding where to locate new conservation areas, and in evaluating the full scope of ecological effects of new projects that would increase nitrogen deposition rates.

Introduction

Soil nitrogen is an important determinant of plant community productivity, diversity and invasibility (Chapin, Vitousek & Van Cleve 1986; Wedin & Tilman 1996). Increased levels of soil nitrogen caused by atmospheric nitrogen deposition can increase the dominance of invasive alien plants and decrease the diversity of plant communities world-wide (Vitousek *et al.* 1997). Where nitrogen levels are naturally low, such as in deserts, relatively small increases in nitrogen may cause large changes in plant communities, because the ratio of increased nitrogen to plant biomass is higher compared with ecosystems with higher plant productivity (Aber *et al.* 1989).

Human population levels are increasing rapidly in the Mojave Desert of North America, making it one of fastest growing regions in the USA (United States Census Bureau 2000). Along with increased human populations will come increased levels of atmospheric pollution and nitrogen deposition. Increased nitrogen deposition has led to increased levels of soil nitrogen in semi-arid coastal sage scrub adjacent to the Mojave Desert (Padgett *et al.* 1999). Levels of soil nitrate and ammonium were also shown to increase 700% (1–8 p.p.m.) and 500% (2–12 p.p.m.), respectively, during summer and through to mid-winter near an urban desert area where air pollution and atmospheric nitrogen levels were high (M. Allen, unpublished data). In comparison, soil nitrate and ammonium levels did not increase during the same time interval at an otherwise similar desert site where air pollution and atmospheric nitrogen levels were low. It is suggested, therefore, that increased atmospheric nitrogen from air pollution can increase soil nitrogen levels. If this happens in the Mojave Desert, then it may cause plant community changes.

The abundance of soil nitrogen varies naturally between microhabitats in desert shrublands. Soils beneath the canopy of desert shrubs represent islands of greater soil nutrients compared with the surrounding interspaces (Garcia-Moya & McKell 1970; Halvorson & Patten 1975; Parker *et al.* 1982; Schlesinger *et al.* 1996). In the Mojave Desert, levels of nitrogen and phosphorous can be 50% higher beneath the north side of *Larrea tridentata* (DC.) Cov. (creosote bush) canopies than in interspaces (Brooks 1998). Nitrogen limitations in deserts may be lower where soil nitrogen is relatively

high beneath woody shrubs compared with the interspaces between them (Romney, Wallace & Hunter 1978) and during years of low productivity when water may be more limiting to plant growth (Gutierrez & Whitford 1987). Accordingly, nitrogen additions may have different effects beneath shrubs than in interspaces and during years of high compared with low plant productivity.

Increased soil nitrogen may have different effects on native and alien annual plants in desert regions. Native plants of low fertility ecosystems such as deserts generally have lower maximal growth rates and respond less to increased soil nutrients than plants that have evolved in more fertile ecosystems (Grime 1977; Chapin, Vitousek & Van Cleve 1986). Many of the common alien annual plant taxa in the Mojave Desert (e.g. *Bromus* spp. and *Erodium cicutarium*) evolved in more fertile Mediterranean regions (Brooks 2000a; Jackson 1985) and may therefore benefit more than native desert annuals from increased levels of soil nitrogen. Effects of increased nitrogen may also differ among these alien plant species because of differing life-history characteristics (Lodge 1993; Brooks 1999a). In addition, increased density and biomass of alien annuals created in response to increased soil nitrogen may heighten competition for soil moisture, potentially decreasing density, biomass and diversity of native annual plants.

The purpose of this study was to evaluate how increased levels of soil nitrogen affect annual plant communities in the Mojave Desert. It was predicted that alien plants would increase in density, biomass and species richness in response to increased nitrogen, and that the net effect on natives would be negative. It was also predicted that the effects of increased nitrogen would be greater where soil nitrogen is naturally low in interspaces compared with where it is naturally high beneath creosote bush canopies, and that the effects would be greater during a year of high annual plant productivity than a year of low productivity.

Materials and methods

STUDY SITES

Three 1-ha sites were established within the central (35°07'30"N, 117°07'45"W), southern (34°41'30"N, 116°57'30"W) and western (35°14'30"N, 117°51'15"W) Mojave Desert. Distances between the sites ranged from 51 to 102 km. To choose the site within each region, a 1-mile² (259-ha) township section was selected randomly from among those owned by the United States Department of the Interior, Bureau of

Land Management, and the study site was located where it was accessible via an unpaved road. All sites contained a creosote bush-dominated plant community with an understorey of winter annual plants growing on granitic, sandy loam soils. More details of the study sites are reported in Brooks (2000b).

Three alien annual plant taxa dominated each site, including the forb *Erodium cicutarium* (L.) L'Hér and the grasses *Bromus madritensis* ssp. *rubens* (L.) Husnot (hereafter called *B. rubens*) and *Schismus* spp., comprising *Schismus arabicus* Ness. and *Schismus barbatus* (L.) Thell. The latter two species are closely related (Faruqi & Quraish 1979; Faruqi 1981) and difficult to distinguish reliably (Brooks 2000c) so they were combined for analysis in this study. Overall, the composition of *Schismus* spp. was estimated to be 75% *S. barbatus* and 25% *S. arabicus*.

Long-term rainfall patterns at each site were estimated by averaging the linear distance-weighted monthly precipitation averages from the three closest National Oceanic and Atmospheric Administration weather stations (National Oceanic and Atmospheric Administration 1996). Rainfall patterns during the study were determined by recording rainfall every 2 weeks from November to April during each year of the study using a single rainfall gauge located at the centre of each site. The amount and temporal distribution of rainfall was similar at the three study sites but differed between 1996 and 1997 (Brooks 2000b). Winter rainfall (October–April) was 94% of the average prior to spring 1996, and 77% of the average prior to spring 1997. However, 46 mm, of the total 67 mm of winter rainfall during 1997, occurred during December, 307% of the monthly average. This pulse of December rainfall resulted in mass germination and higher productivity and diversity of the seedling cohort during 1997, even though total rainfall was higher in 1996.

EXPERIMENTAL TREATMENTS

Three treatments consisted of nitrogen added as ammonium nitrate (NH_4NO_3), nitrogen added as 15-15-15 (NPK) fertilizer, and an unfertilized control. The NPK fertilizer treatment was included because availability of phosphorous can limit plant growth in some desert soils (Lajtha & Schlesinger 1988; DeLucia, Schlesinger & Billings 1989). Fertilizers were added in dry, water-soluble form to minimize the chance of burning foliage and leaching downward through the soil profile. The 2–4-mm diameter pellets remained in place at the soil surface even when subjected to high winds (M. Brooks, personal observation).

The rate of nitrogen application ($3.2 \text{ g N m}^{-2} \text{ year}^{-1}$) was similar to maximum rates of atmospheric nitrogen deposition adjacent to the Mojave Desert in chaparral shrublands of the Los Angeles basin ($3.0 \text{ g N m}^{-2} \text{ year}^{-1}$) (Bytnerowicz *et al.* 1987). Ammonium nitrate and NPK treatments were added in two equal amounts (1.6 g N m^{-2} each) on 27–29 December 1995 and 6 March

1996 during the first year, and 20 December 1996 and 13 February 1997 during the second year.

EXPERIMENTAL DESIGN

Three experimental treatments (NH_4NO_3 , NPK, control) were replicated in 25 blocks at each of the three study sites in a randomized complete block design with no replication within blocks (Steel & Torrie 1980). The blocks were arranged in a 5×5 grid with an average of 25 m between each block (1 ha total area for each site). Each block was centred on a creosote bush with ≥ 150 cm canopy diameter and contained two microhabitats, the area beneath the canopy on the north side of the creosote bush (beneath-canopy) and the adjacent open space ≥ 1 m from the canopy edge (interspace). Three 40×50 -cm contiguous plots were established in each microhabitat, each randomly receiving a different treatment. Treatments were repeated in the same plots during the second year. The 150-cm minimum creosote bush canopy diameter allowed enough room to fit the treatment plots completely within the beneath-canopy microhabitat.

The response of native annuals to fertilization was evaluated by sampling annual plants when winter annuals reached peak biomass and most species were flowering and setting seed. This occurred from 10 to 18 April 1996 and 9 to 17 March 1997. In each 40×50 -cm treatment plot, live annual plants were clipped at ground level within a 10×20 -cm (200 cm^2) sampling frame, sorted and counted by species, dried to a constant mass at 60°C , and weighed to determine above-ground live dry biomass. Species were identified using Hickman (1993). Species richness was calculated as the number of species within each biomass sample. Samples collected during the second year were located 20 cm from the first-year samples, within each treatment plot.

DATA ANALYSES

Repeated-measures analysis of variance (rMANOVA) was used to evaluate main and interactive effects of fertilization on annual plants during 1996 and 1997 (SAS 1988). ANOVA models included all main and interactive effects of treatment, microhabitat and year. Data were pooled from the three sites in all analyses because interactions of site-by-treatment, site-by-microhabitat, site-by-treatment-by-microhabitat and site-by-treatment-by-microhabitat-by-year were not significant (rMANOVA, $P < 0.300$; Underwood 1997).

The data were analysed in three steps, all using the full model plus additional factors and their interactions with treatment. First, to evaluate differential responses of alien and native plant density, biomass and species richness, a group factor was added (native, alien). Secondly, to evaluate the differential responses among the most abundant alien species, the group factor was replaced with a species factor (*B. rubens*,

Table 1. Annual plant species sampled at the three study sites

Species*		No. of sites	Species		No. of sites
<i>Amsinckia tessellata</i>	NF	3	<i>Gilia minor</i>	NF	3
<i>Astragalus didymocarpus</i>	NF	3	<i>Guillenia lasiophylla</i>	NF	3
<i>Bromus rubens</i>	AG	3	<i>Lasthenia californica</i>	NF	3
<i>Bromus tectorum</i>	AG	3	<i>Layia glandulosa</i>	NF	2
<i>Bromus trinitii</i>	AG	2	<i>Linanthus dichotomus</i>	NF	3
<i>Camissonia campestris</i>	NF	3	<i>Lotus humistratus</i>	NF	3
<i>Camissonia claviformis</i>	NF	2	<i>Lupinus odouratus</i>	NF	2
<i>Chenactis fremontii</i>	NF	3	<i>Malacothrix coulteri</i>	NF	3
<i>Chenactis steviodes</i>	NF	3	<i>Malacothrix glabrata</i>	NF	3
<i>Chorizanthe brevicornu</i>	NF	3	<i>Monoptilon belliflorae</i>	NF	3
<i>Chorizanthe watsonii</i>	NF	3	<i>Oxytheca perfoliata</i>	NF	3
<i>Coreopsis bigelovii</i>	NF	3	<i>Pectocarya</i> spp.	NF	3
<i>Crypthantha circumcissa</i>	NF	3	<i>Phacelia distans</i>	NF	1
<i>Crypthantha dumetorum</i>	NF	3	<i>Phacelia fremontii</i>	NF	3
<i>Crypthantha nevadensis</i>	NF	3	<i>Phacelia tanacetifolia</i>	NF	3
<i>Crypthantha pterocarya</i>	NF	3	<i>Salvia columbariae</i>	NF	2
<i>Descurainia pinnata</i>	NF	3	<i>Schismus arabicus</i>	AG	3
<i>Eremalche exilis</i>	NF	1	<i>Schismus barbatus</i>	AG	3
<i>Eriophyllum wallacei</i>	NF	3	<i>Stephanomeria parryi</i>	NF	3
<i>Erodium cicutarium</i>	AF	3	<i>Vulpia microstachys</i>	NG	3
<i>Escholtzia minutiflora</i>	NF	3	<i>Vulpia octoflora</i>	NG	3
<i>Filago californica</i>	NF	3			

*AF, alien forb; AG, alien grass; NF, native forb; NG, native grass.

Schismus spp., *E. cicutarium*). Thirdly, to evaluate the individual responses of these alien species, density and biomass of each were analysed separately.

When overall effects were significant levels within each factor were compared using Fisher's protected least significant difference (Day & Quinn 1989). Because all effects except block were fixed, the significance of each was tested using the block-factor interaction as the error term. Data were transformed prior to analysis for species richness and density using square root ($x + 0.5$), for biomass using log ($x + 1$), and for proportions using arcsin (square root x) (Sokal & Rohlf 1995). Data were reported as untransformed values, and effects were considered significant at $P < 0.050$. Bonferroni-corrected P -values were used when comparing the individual effects of alien species.

Results

Forty-three annual plant species were sampled, ranging from 38 to 41 species per site (Table 1). Of these species, 35 were native forbs, two were native grasses, one was an alien forb and five were alien grasses. It should be noted that *S. arabicus* and *S. barbatus* were pooled into *Schismus* spp. prior to analysis, resulting in four alien grass taxa (five total alien taxa) used to calculate alien species richness.

Bromus rubens, *Schismus* spp. and *E. cicutarium* were the most abundant alien species, comprising 95% of the total alien plant density and 98% of the total alien plant biomass combined across all sites and treatment plots. *Amsinckia tessellata* A. Gray, *Descurainia pinnata* (Walter) Britton, *Guillenia lasiophylla* (Hook. & Arn.)

Table 2. Density, biomass and species richness of annual plants in 0.02-m² plots. This repeated-measures analysis of variance table shows treatment effects (control, ammonium nitrate, NPK) and interactions with microhabitat (Larrea-north, Larrea-south, interspace), group (aliens, natives) and the repeated factor year (1996, 1997). F -ratios were calculated with the block-by-effect interaction as the error term. Significant P -values are in italic (< 0.05)

Source	$F_{2,148}$	P
Density		
Treatment	1.88	0.157
Treatment $\times$ microhabitat	2.79	0.064
Treatment $\times$ group	6.14	<i>0.003</i>
Treatment $\times$ microhabitat $\times$ group	2.30	0.104
Year $\times$ treatment	1.16	0.316
Year $\times$ treatment $\times$ microhabitat	0.17	0.843
Year $\times$ treatment $\times$ group	1.07	0.347
Year $\times$ treatment $\times$ microhabitat $\times$ group	0.46	0.634
Biomass		
Treatment	75.61	<i>< 0.001</i>
Treatment $\times$ microhabitat	2.71	0.070
Treatment $\times$ group	80.50	<i>< 0.001</i>
Treatment $\times$ microhabitat $\times$ group	4.37	<i>0.014</i>
Year $\times$ treatment	26.04	<i>< 0.001</i>
Year $\times$ treatment $\times$ microhabitat	10.39	<i>< 0.001</i>
Year $\times$ treatment $\times$ group	31.81	<i>< 0.001</i>
Year $\times$ treatment $\times$ microhabitat $\times$ group	8.97	<i>< 0.001</i>
Species richness		
Treatment	15.62	<i>< 0.001</i>
Treatment $\times$ microhabitat	0.97	0.383
Treatment $\times$ group	16.15	<i>< 0.001</i>
Treatment $\times$ microhabitat $\times$ group	1.09	0.339
Year $\times$ treatment	17.77	<i>< 0.001</i>
Year $\times$ treatment $\times$ microhabitat	2.85	0.061
Year $\times$ treatment $\times$ group	12.04	<i>< 0.001</i>
Year $\times$ treatment $\times$ microhabitat $\times$ group	0.73	0.483

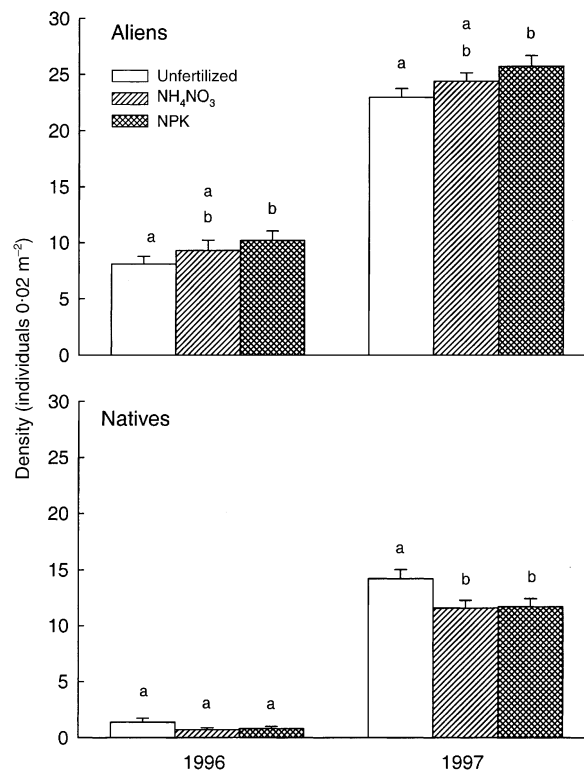


Fig. 1. Density of annual plants after experimental treatments in April 1996 and March 1997. Values are averages ($n = 150$, ± 1 SE) and dissimilar letters within years and groups indicate significant differences within each year using Fisher's protected LSD ($P < 0.05$).

E. Greene, *Malacothrix coulteri* A. Gray and *Phacelia tanacetifolia* Benth. were the most abundant native annuals in the beneath-canopy microhabitat. *Amsinckia tessellata*, *Filago californica* Nutt. *Lasthenia californica* Lindley and *Pectocarya* spp. were the most abundant natives in the interspace microhabitat.

EFFECTS OF TREATMENTS ON ALIENS AND NATIVES

The total density of annual plants was not significantly affected by nutrient treatments (treatment-by-group interaction; Table 2), due to the contrasting responses of aliens and natives (Fig. 1). Alien plant density increased whereas native density decreased in response to nutrient additions, and effects were similar for ammonium nitrate and NPK fertilizer. Treatment effects did not differ significantly between microhabitats or years (Table 2).

Total biomass of annuals was significantly affected by nutrient treatments, and effects varied between aliens and natives (Table 2). The effects of fertilizer treatments were similar, and their average effects resulted in 56% and 52% increases in alien biomass, and 37% and 42% decreases in native biomass, during 1996 and 1997, respectively (Fig. 2). Treatment effects did not differ significantly between microhabitats but did differ between years (Table 2).

Species richness of annual plants was significantly affected by nutrient treatments, and the effects differed

between aliens and natives (Table 2). Alien species richness was unaffected by treatments during both years, possibly because there were only three alien species present, and control plots averaged 1–2 alien species even without nutrient additions. In contrast, native species richness was significantly reduced by nutrient treatments but only in 1997 when the seedling cohorts comprised a wide range of species (Fig. 3). Effects were similar for the two fertilizer treatments. Treatments did not differ significantly among microhabitats but did vary between years (Table 2).

EFFECTS OF TREATMENTS ON INDIVIDUAL ALIEN SPECIES

Among these three most abundant alien species, *B. rubens*, *Schismus* spp. and *E. cicutarium*, nitrogen treatment effects were not significantly different for density (treatment-by-species interaction, $F_{2,148} = 0.60$, $P = 0.668$) but were significantly different for biomass (treatment-by-species, $F_{2,148} = 18.16$, $P < 0.001$). Biomass effects among alien species also varied between microhabitats (treatment-by-species-by-microhabitat, $F_{2,148} = 52.34$, $P < 0.001$) and between years (treatment-by-species-by-year, $F_{2,148} = 12.25$, $P < 0.001$). Thus, nutrient treatments had a stronger effect on alien biomass than density, and effects on alien biomass differed between microhabitats and years.

Responses of each alien species to nitrogen treatments differed between microhabitats and between years.

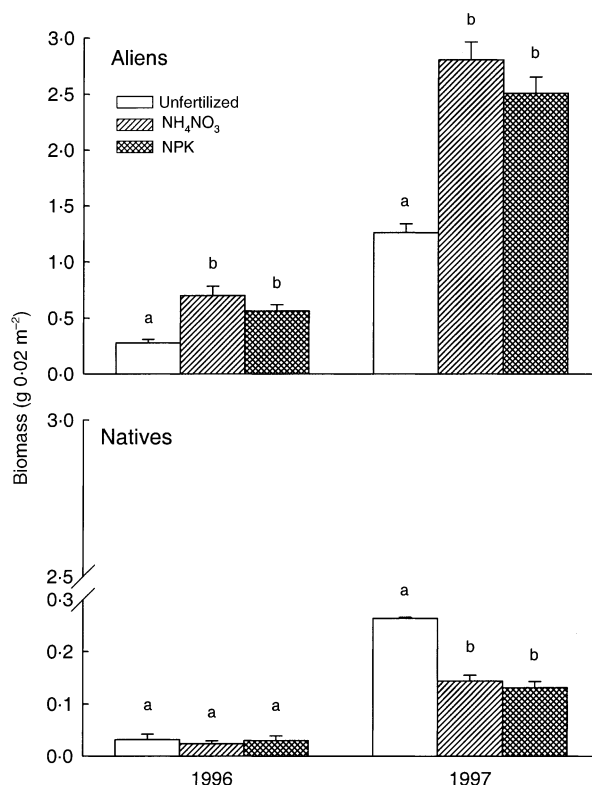


Fig. 2. Biomass of annual plants after experimental treatments in April 1996 and March 1997. Values are averages ($n = 150$, $+1$ SE) and dissimilar letters indicate significant differences within each year using Fisher's protected LSD ($P < 0.05$).

Bromus rubens biomass was higher, and its response to nutrient treatments was stronger, where soil nutrient levels were naturally high in the beneath-canopy microhabitat compared with the interspace microhabitat (Table 3 and Fig. 4). Effects on *B. rubens* were similar for ammonium nitrate and the NPK fertilizers. In contrast, *Schismus* spp. and *Erodium cicutarium* biomasses were higher, and their response to nutrient treatments were stronger where soil nutrient levels were naturally low in the interspace microhabitat. Although effects of the two nutrient treatments were similar, biomass of *Schismus* spp. was highest with NPK fertilizer and biomass of *E. cicutarium* was highest with ammonium nitrate (Fig. 4). Nutrient treatments significantly increased biomass of aliens during both years (Fig. 4). However, effects were generally stronger during 1997 than 1996, especially for *B. rubens* biomass (Table 3 and Fig. 4).

Discussion

Alien plants comprise a relatively small proportion of desert floras world-wide (Lonsdale 1999), possibly because many invasive species cannot survive the low soil moisture and nitrogen levels found in desert regions. This study demonstrated that soil nitrogen addition can increase the dominance of alien annual plants in the Mojave Desert. The increased biomass of alien plants and decreased biomass of natives also suggests that aliens may have higher seed production than natives in response to increased nitrogen, because plant

Table 3. Absolute biomass (grams) of individual alien annual plant species in 0.02-m² plots. This repeated-measures analysis of variance table shows treatment effects (control, ammonium nitrate, NPK) and interactions with microhabitat (Larrea-north, Larrea-south, interspace) and the repeated factor year (1996, 1997). *F*-ratios were calculated using the block-by-effect interaction as the error term. Significant *P*-values are in *italic* (< 0.05)

Source	<i>F</i> _{2,148}	<i>P</i>
<i>Bromus rubens</i>		
Treatment	36.84	<i>< 0.001</i>
Treatment × microhabitat	32.22	<i>< 0.001</i>
Year × treatment	21.45	<i>< 0.001</i>
Year × treatment × microhabitat	18.93	<i>< 0.001</i>
<i>Schismus</i> spp.		
Treatment	18.45	<i>< 0.001</i>
Treatment × microhabitat	15.59	<i>< 0.001</i>
Year × treatment	3.71	0.027
Year × treatment × microhabitat	3.47	0.034
<i>Erodium cicutarium</i>		
Treatment	56.52	<i>< 0.001</i>
Treatment × microhabitat	56.26	<i>< 0.001</i>
Year × treatment	4.23	0.016
Year × treatment × microhabitat	3.26	0.041

biomass and fecundity are positively correlated (Cousens & Mortimer 1995). These results indicate that moderate increases in soil nitrogen ($3.2 \text{ g N m}^{-2} \text{ year}^{-1}$) that are comparable to observed rates of atmospheric nitrogen deposition in adjacent semi-arid shrublands near more urbanized areas ($3.0 \text{ g N m}^{-2} \text{ year}^{-1}$) (Bytnerowicz

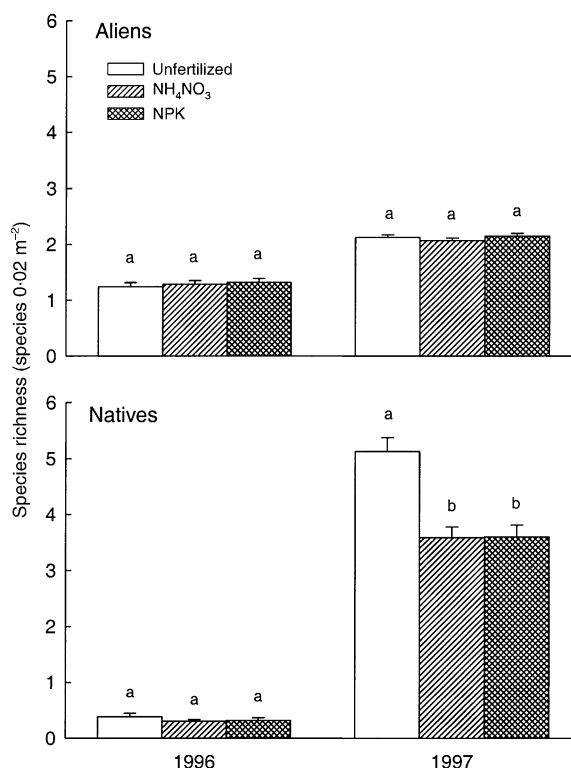


Fig. 3. Species richness of annual plants after experimental treatments in April 1996 and March 1997. Values are averages ($n = 150$, ± 1 SE) and dissimilar letters indicate significant differences within each year using Fisher's protected LSD ($P < 0.05$).

et al. 1987) can significantly affect annual plant communities in the Mojave Desert.

Biomass of the alien annual grass *S. arabicus* also increased relative to native species after addition of nitrogen at a desert site in Chile (Gutierrez, Aguilera & Armesto 1992). Similar experiments were conducted in the northern Mojave Desert from 1967 to 1975, but aliens were uncommon at that time and significant densities of *B. rubens* and *S. arabicus* did not appear until 1975, when their densities were still $< 5\%$ of those observed in the current study (Romney, Wallace & Hunter 1978). Fertilization with nitrogen ($10 \text{ g N m}^{-2} \text{ year}^{-1}$) increased biomass of native annuals from 130% for *Chaenactis fremontii* A. Gray to 716% for *Amsinckia tessellata* (Romney, Wallace & Hunter 1978). These same two species were present in the current study, and *Amsinckia tessellata* was one of the most abundant, but increased soil nitrogen did not significantly increase either their density or biomass (M. Brooks unpublished data). These results suggest that native desert annuals may benefit from increased nitrogen when aliens are scarce, but may not benefit when aliens are abundant.

Decreased native annual plant density, biomass and species richness caused by increased soil nitrogen levels may have been due to increased competition with alien species for soil water and other nutrients. Native seedlings senesced approximately 1–2 weeks earlier than alien seedlings on fertilized compared with unfertilized plots in the current study (M. Brooks, personal observation). Natives also senesced 2 weeks sooner

than alien species where the net competitive effect of aliens was stronger on unthinned plots, compared with plots that were thinned of aliens at the same sites and during the same years as the current study (Brooks 2000b). Wilson, Harris & Gates (1966) found that nitrogen additions increased *Bromus* yields and led to competitive suppression of the native bunchgrass *Agropyron spicatum*. Melgoza & Nowak (1991) showed that *B. tectorum* extracts soil water at a faster rate than native shrub seedlings, resulting in its competitive superiority in post-fire landscapes. Increased biomass of alien annual plants caused by elevated soil nutrient levels may increase their competitive effects on natives, thereby decreasing their abundance and leading to a decrease in species richness of native annual plants.

The competitive effects of aliens on native desert plants should be most apparent during years when native plants germinate in large numbers (Brooks 2000b). Native annuals typically remain dormant for many years until sufficient rainfall stimulates germination (Beatley 1974). The large differences in density and biomass of natives between 1996 and 1997 in the current study was a result of sufficient rainfall for mass germination only occurring prior to spring 1997 (Brooks 2000b). However, increases in native plant density and biomass between the first and second years were significantly lower in nitrogen-addition plots, where alien abundance was highest, compared with control plots. The ability of native annual plants to respond to ephemeral rainfall events with the increased growth and reproduction necessary to maintain their

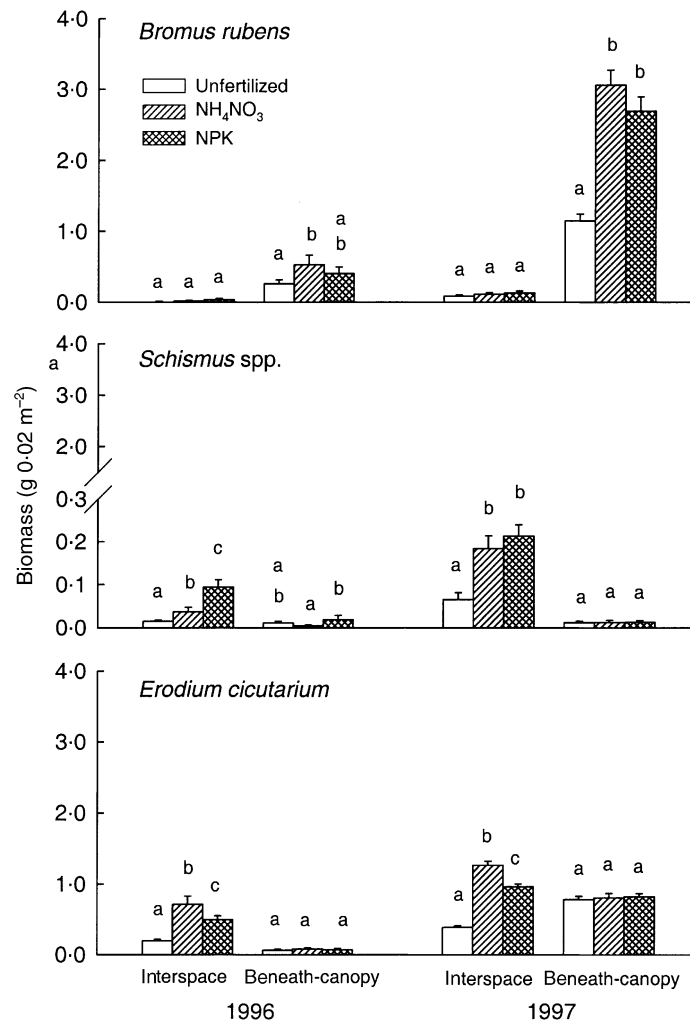


Fig. 4. Biomass of three alien annual plant species after experimental treatments in April 1996 and March 1997. Values are averages ($n = 75$, $+1$ SE) and dissimilar letters indicate significant differences within each microhabitat within each year using Fisher's protected LSD ($P < 0.05$).

populations may be hindered by increased alien plant growth stimulated by soil nitrogen additions.

Annual plants that are alien to desert regions typically do not have strict germination requirements and germinate in response to much less rainfall than native species (Beatley 1966; Vidiella & Armesto 1989; Gutierrez 1992). As a result differences in density and biomass of aliens between 1996 and 1997 were not nearly as dramatic as those observed for native annuals. The ability of alien species to germinate during years of low rainfall allows them to utilize soil nitrogen at a time when most native annuals remain dormant as seeds. The danger in germinating after small rainfall events is that there may not be enough residual soil moisture to support plant growth, and seedlings may die before reproducing. This vulnerability may be more acute for *B. rubens*, which evolved in mesic and semi-arid Mediterranean regions, than for *Schismus* spp. or *E. cicutarium*, which evolved in more arid regions (Brooks 1999a).

Increased soil nitrogen levels are thought to affect annual plants only during years of moderate or high

rainfall in desert regions (Romney, Wallace & Hunter 1978; Gutierrez 1992). The current study suggests that this is true for native desert annuals but that increased nitrogen levels may affect alien annuals during all but the driest years. In addition, this study provides evidence that patterns of rainfall within years may be more important than annual rainfall totals in predicting germination events and effects of nitrogen on desert annual plant communities. Despite lower rainfall in 1997, annual plant productivity was higher and the responses of annual plants to nitrogen addition were stronger compared with 1996, due to very high rainfall events during December that triggered germination of annual plants. Thus, extreme rainfall events rather than seasonal averages should be considered when evaluating the potential magnitude of annual plant responses to increased levels of soil nitrogen.

Nitrogen limitations for plant growth in desert regions are also thought to be greater where soil nitrogen levels are naturally low in the interspaces between shrubs, than where they are naturally high beneath shrub canopies (Romney *et al.* 1974). Nitrogen additions

should therefore have the greatest effects on annual plants in interspaces, where they would cause the highest percentage increase in soil nitrogen. Results of the current study indicate that this is not always true, and that increased nitrogen can increase annual plant biomass in both microhabitats although individual species may respond differently. For example, effects of nitrogen treatments were highest in the beneath-canopy for *B. rubens* and in interspaces for *Schismus* spp. and *E. cicutarium*.

MANAGEMENT IMPLICATIONS OF INCREASED SOIL NITROGEN

As human populations and air pollution levels increase in the Mojave Desert and other desert regions, nitrogen deposition from atmospheric pollutants will probably increase soil nitrogen levels, causing potentially dramatic changes in annual plant communities. Productivity and reproduction rates of alien annual plants could increase at the expense of native annuals that may be at a competitive disadvantage. Years of nitrogen deposition may cause directional shifts in desert annual plant communities towards increased dominance by alien species and decreased diversity of native species.

Nitrogen deposition may have synergistic effects with other forms of disturbance. For example, surface disturbances caused by grazing, off-highway vehicle use or construction of linear corridors for roads or pipelines could facilitate the invasions and establishment of alien plants that may in turn respond to increased levels of soil nitrogen. Increased productivity of alien annual grasses caused by atmospheric nitrogen deposition, especially during years of high rainfall, may also affect desert fire regimes. Alien annual grasses produce large amounts of continuous fine fuels that facilitate the spread of fire where fires were historically infrequent (Rogers & Vint 1987; D'Antonio & Vitousek 1992; Brooks 1999b). Post-fire desert landscapes are often dominated by alien annual grasses, creating conditions that promote recurrent fire (Brooks & Pyke 2001). Thus, nitrogen deposition could facilitate changes in desert fire regimes by increasing productivity of alien annual grasses.

Management of atmospheric nitrogen deposition requires a regional approach that is often beyond the control of local land managers. However, these managers need to understand the potential effects of nitrogen deposition on desert ecosystems, and in particular how these effects may interact with land-use activities that they can manage. Additional studies are needed to determine these relationships, and to evaluate the relative ecological impact of nitrogen deposition compared with other forms of disturbance in desert ecosystems.

New conservation areas should be located where current and projected future rates of nitrogen deposition are low, whenever possible. Examples of such sites

would be far removed, or at least downwind, from major sources of atmospheric nitrogen pollutants. The evaluation of environmental threats posed by new projects that would increase the production of nitrogen pollutants should consider their potential to increase the dominance of invasive alien plants and to facilitate the invasion of new alien species.

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