



Habitat invasibility and dominance by alien annual plants in the western Mojave Desert

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Abstract

Patterns of habitat invasibility and alien dominance, respectively measured as species richness and biomass of alien annual plants, were evaluated in association with four habitat factors at the Desert Tortoise Research Natural Area (DTNA) in the western Mojave Desert, USA. Habitat factors varied in levels of disturbance outside (high) and inside (low) the DTNA, and in levels of soil nutrients in washlet (high) and hummock (low) topographic positions, in *Larrea*-north (high), *Larrea*-south (medium), and interspace (low) microhabitats near creosote bushes (*Larrea tridentata*), and during 1995 when rainfall was 207% (high) and 1994 when rainfall was 52% (low) of the long-term average. Dominant alien plants included the annual grasses *Bromus rubens*, *Bromus trinii*, and *Schismus* spp., and the forb *Erodium cicutarium*. Species richness and dominance of alien annual plants were slightly higher where disturbance was high, and much higher where soil nutrients were high. *B. rubens* and *B. trinii* were most dominant in washlets and in the *Larrea*-north microhabitats during both years. These two species evolved in mesic ecosystems, and appeared to be particularly limited by soil nutrients at this site. *Schismus* spp. and *E. cicutarium* were also most dominant in washlets, but their dominance varied between interspaces in 1994 and the *Larrea*-south microhabitat in 1995. Monitoring to detect the invasion of new annual plants should focus on regions of high rainfall and nitrogen deposition and on washes and beneath-canopy microhabitats. The ecological range of each alien species should be evaluated separately, because their evolutionary origins may greatly affect their patterns of invasion and dominance in the Mojave Desert.

Introduction

The ease with which plant invasions occur is often termed invasibility, and is typically measured as the number of alien species in an area (alien richness). In general, alien richness is highest at intermediate levels of soil nutrients (Tilman 1988; Huenneke et al. 1990; Hobbs and Huenneke 1992) and at high levels of disturbance (Elton 1958; Grime 1979; Huston 1979; Hobbs 1989), especially anthropogenic disturbance (Rejmánek 1989). Soils with high levels of mineral nutrients and water often support high cover of

competitive native species that hinder the establishment of invading plants, whereas low nutrient soils often require phenotypic specializations or tolerances of low resource levels that few alien plants possess. Disturbances can reduce cover of competitive natives, thereby increasing opportunities for aliens to become established (Huston 1994). The combined effects of disturbance and soil nutrients in particular can facilitate plant invasions.

Another characteristic of plant invasions is alien dominance, which is typically measured as the amount of alien biomass in a community. In contrast to alien

richness, generalized patterns of alien biomass among ecosystems and within habitats are poorly described. A plant community can be dominated by aliens, but still be considered relatively uninvasible if it contains few alien species. It is unclear if the processes that maximize alien richness also maximize alien biomass, and patterns of habitat invasibility and alien dominance may differ in association with levels of soil nutrients and disturbance. Simultaneous measurement of both alien richness and biomass at different levels of soil nutrients and disturbance are required to compare these differences.

The Mojave Desert of southwestern North America is a good ecosystem in which to study the relationships of habitat invasibility and alien dominance with levels of soil nutrients and disturbance. Although overall levels of disturbance and soil nutrients are low, they can vary significantly at small scales. Locally high levels of livestock grazing (Webb and Stielstra 1979; Nicholson and Humphreys 1981) and off-highway vehicle (OHV) use (Davidson and Fox 1974; Vollmer et al. 1976; Webb and Wilshire 1983) cause variation in anthropogenic disturbance, and fenced ecological reserves provide distinct contrasts between disturbed and undisturbed areas (Brooks 1995, 1999). Soil nutrients such as nitrogen, phosphorous, and water vary among topographic positions in deserts where they are more abundant in run-on areas such as washes than run-off areas such as hummocks (MacMahon and Schimpf 1981; Pickup 1985; Stafford-Smith and Morton 1990). Soil nutrients also vary among microhabitats created by large woody shrubs. Nutrients are more abundant beneath shrub canopies compared to interspaces (Garcia-Moya and McKell 1970; Halvorson et al. 1994; Schlesinger et al. 1996), and in the Mojave Desert they can also be higher beneath the north canopy than the south canopy (Samson 1986; Brooks 1998). Availability of water also varies temporally, with greater amounts during years of high than low rainfall.

Because overall levels of soil nutrients in the Mojave Desert are low relative to other ecosystems (Rundel and Gibson 1996), the high nutrient concentrations that produce high cover of competitive natives that hinders the establishment and growth of aliens may never be found in this region. Hence, the positive combined effects of high disturbance and soil nutrient levels may be less important in promoting plant invasions in this ecosystem compared to others.

I compared conditions associated with habitat invasibility and alien dominance at a site in the western

Mojave Desert. Disturbance levels varied between the inside and outside of the Desert Tortoise Research Natural Area (DTNA), an area managed by the Bureau of Land Management, California Department of Fish and Game, and the Desert Tortoise Preserve Committee, Inc. Soil nutrient levels varied spatially among topographic positions and microhabitats, and temporally among rainfall years. I focused on the annual plant community because alien annuals are the most widespread, common, and diverse group of alien plants in this region (Kemp and Brooks 1998). Because patterns of plant invasions often vary among species (Lodge 1993), I evaluated the dominance of alien annuals both as a group and individually. I predicted that alien richness and biomass would be higher where disturbance was higher outside than inside the DTNA, where soil nutrients were higher on the north side of shrubs than the south side or interspaces and in washlets than hummocks, and following a winter of high compared to low rainfall. I also evaluated the interactive effects of disturbance with each of the three soil nutrient factors.

Methods

Study site

The 10,100 ha DTNA is located in the Fremont Valley and Rand Mountains of the western Mojave Desert, adjacent to California City, Kern County, California (34°15' lat. 117°50' long.). The DTNA is approximately 30 km east of the foothills of the Sierra Nevada Mountains and receives more rainfall than areas farther east in the western and central Mojave Desert (NOAA 1995). Average annual rainfall at this site is 157 mm, 87% occurring from October through April inclusive (Figure 1). Mid-summer temperatures in August range from an average low of 19°C to an average high of 34°C, and mid-winter temperatures in December range from an average low of 0°C to an average high of 7°C.

Sheep have grazed the western Mojave Desert since the late 1800s when more than 500,000 used this range annually, compared to about 25,000 today (BLM 1980, 1993). Off-highway vehicle use has been prevalent since the 1960s and up until its creation the DTNA was open to unlimited OHV travel (Adams et al. 1982; BLM 1980). The DTNA was established and closed to OHVs in 1973, and was closed to livestock grazing in 1976. A 1 m tall fence of 15 × 15 cm welded wire

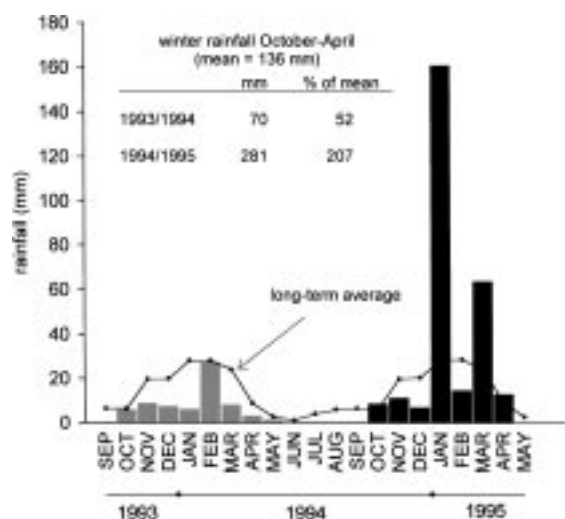


Figure 1. Monthly rainfall at the DTNA. Data were calculated from linear distance-weighted means of the two closest NOAA weather stations located 21 km NE in Randsburg and 40 km SW in Mojave. Long-term averages were based on 59 years of data collected at Randsburg and 94 years at Mojave.

was constructed from 1977–1980 around the perimeter (BLM and CDFG 1988). This fence has protected the DTNA from disturbance by humans and livestock, while allowing native animals to pass freely, for 14 years prior to the beginning of this study. Grazing and OHV use continues to occur outside the DTNA, especially during the Spring months. Additional information on the disturbance history of this site is reported in Brooks (1999).

Approximately 75 ha of the DTNA and an equal amount of adjacent unprotected land were studied (~150 ha). Elevation at this site ranged from 870 to 915 m and the topography was southwest-facing with 0–15% slope. The soil was Randsburg sandy loam composed of well-drained gravelly residual soils less than 30 cm deep over a granitic pediment (Valverde and Hill 1981). The woody plant community was dominated by *Larrea tridentata* and *Ambrosia dumosa* with *Xylorhiza tortifolia*, *Lycium andersonii*, *Psoralea fremontii*, and *Acamptopappus sphaerocephalus* as sub-dominants (Brooks 1995). No alien perennial plants were present.

Winter annuals dominated the flora of the DTNA, and the most common alien species included the forb *Erodium cicutarium* and annual grasses in the genera *Schismus* and *Bromus*. These aliens followed similar phenological patterns as the native annuals,

germinating during winter and senescing by mid-spring. *Schismus arabicus* and *Schismus barbatus* are closely related and difficult to distinguish (Faruqui and Quraish 1979; Faruqui 1981; Brooks 2000a), so they were combined into *Schismus* spp. in this study. *Bromus madritensis* subsp. *rubens* (hereafter called *Bromus rubens*), *Bromus tectorum*, and *Bromus trinii* were also present, although *Bromus tectorum* was relatively uncommon.

Erodium cicutarium has been in California since the 1700s (Heady 1988), and likely in the Mojave Desert since the 1800s. *Schismus* spp., *Bromus rubens*, and *Bromus tectorum* likely arrived during the first half of the 1900s (Brooks 2000a,b), but probably did not become dominant until after 1950 (O. Clarke, personal communication). *Bromus trinii* is a native of Chile and may have arrived in California before the arrival of Europeans (A. Sanders, personal communication), but is generally considered an alien in this region (Hickman 1993). Plant nomenclature followed Hickman (1993).

Sampling design

Inferring past mechanisms from current distributions can be complicated, and always depends on critical assumptions. However, in the absence of controlled experiments, pattern analysis is often the best way to generate and test hypotheses about plant invasions. In this study I evaluated the effects of disturbance and soil nutrients on alien richness and biomass by measuring their current associations at the DTNA. This method assumed that the environmental conditions that promoted invasion had not changed subsequent to invasion. For example, nitrogen-fixing alien plants can increase levels of soil nitrogen (Vitousek 1990) and fire-adapted alien grasses can increase fire return intervals and alter soil nutrient flux rates (D'Antonio and Vitousek 1992), thus confounding interpretation of current patterns. There was no evidence that alien plants had caused any significant changes in soil nutrient or disturbance levels at the DTNA subsequent to invasion. Hence, I assumed that the current associations of alien annual plants with environmental variables could be used to infer the habitat characteristics that promoted their invasion into this site. For most analyses I evaluated absolute alien richness and biomass, because patterns of proportional measures may have been due to increases in aliens, decreases in natives, or some combination of both after invasion.

I evaluated the effects of disturbance on alien richness and dominance by comparing characteristics of the annual plant community inside and outside the DTNA. I established five randomly located blocks separated by > 400 m within the 150 ha study site. Each block consisted of a pair of 1 ha plots, one inside and one outside the DTNA. Each pair was matched for slope, aspect, elevation, topography, and soil type and all plots were located > 150 m from the perimeter fence. Disturbance levels in these paired-plots varied from high (outside) to low (inside). Levels of sheep grazing and OHV use outside the DTNA varied among blocks based on their proximity to watering sites and dirt roads, so the outside plots in each block were characterized by slightly different cumulative levels of disturbance. Thus, the blocks represented five similar but locally distinct disturbance regimes, and not a pseudoreplication of one disturbance regime. Levels of soil nitrogen, phosphorous, and soil depth did not significantly vary, but soil compaction was slightly higher outside (8.70 ± 0.63 kg/cm²) than inside (7.07 ± 0.67 kg/cm²) the DTNA at 2 cm, but not at greater depths (Brooks 1998). Because sheep did not graze outside the DTNA in 1994, and grazed only after sampling was completed in 1995, differences in disturbance were due to the cumulative effects of past grazing and past and current OHV use.

I compared two topographic positions that varied in soil nutrient levels (N, P, H₂O) within each plot. Nutrient levels varied from high in run-on areas in intervening drainages consisting of deep, sandy, alluvial soils (washlet) to low in water run-off areas consisting of shallow, rocky, loamy, residual soils (hummock) (Figure 2). The washlet topographic position was centered on an ephemeral watercourse (≤ 2 m wide), but also extended 5–15 m on either side to include low-lying, deep-soiled alluvial flats. Topographic relief was low and undulating, with adjacent hummocks and washlets separated by ≤ 3 vertical meters. Compared

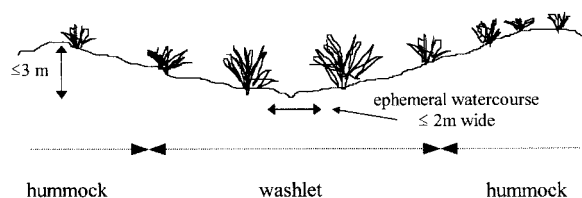


Figure 2. Stylized representations of hummock and washlet topographic positions that are characteristic of the alluvial bajadas in the Mojave Desert.

to hummocks the soils in washlets had similar amounts of nitrogen ($0.092 \pm 0.004\%$, $0.079 \pm 0.004\%$) and phosphorous (21.97 ± 0.84 ppm, 21.90 ± 0.81 ppm), but were deeper (24.1 ± 0.41 cm, 20.9 ± 0.68 cm) and had 70% lower soil compaction (Brooks 1998). Thus, nitrogen and phosphorous levels were similar, but washlets received more water via run-off from hummocks and were more conducive to water infiltration. Disturbances were slightly higher in washlets than hummocks due to ephemeral water flow in the small watercourse located at the center of each washlet (Figure 2). To minimize the differential effects of disturbance, and to focus on soil nutrient differences between the topographic positions, I did not sample within 2 m of any ephemeral watercourse.

I also compared three microhabitats associated with creosote bush (*Larrea tridentata*), the dominant perennial shrub in the Mojave Desert (Rundel and Gibson 1995) and at this site (Brooks 1995). Nutrient levels varied from high beneath the north side of creosote bush canopies (*Larrea-north*), to medium beneath the south side (*Larrea-south*), and to low in the open areas > 1 m from the nearest shrub or perennial grass canopy (interspace). Nitrogen levels were highest in the *Larrea-north* microhabitat ($0.12 \pm 0.003\%$), slightly lower in the *Larrea-south* ($0.10 \pm 0.003\%$), and much lower in the interspace ($0.03 \pm 0.002\%$) (Brooks 1998). Phosphorous levels were also higher in the *Larrea-north* (26.50 ± 0.61 ppm) and *Larrea-south* (26.77 ± 0.64 ppm), and lower in the interspace (11.03 ± 0.49 ppm). Soils were deeper in the *Larrea-north* (23.70 ± 0.53 cm) and *Larrea-south* (23.80 ± 0.58 cm) than interspaces (20.00 ± 0.88 cm), and compaction was approximately 50% lower under creosote bushes than interspaces. Disturbance caused by animal burrowing was often higher under creosote bushes than interspaces, but I minimized this effect by choosing creosote bushes without active burrowing beneath their canopies. Hence, I assumed that the primary difference among microhabitats was due to levels of soil nutrients.

This study was conducted over two years in which rainfall varied from 52% to 207% of the long-term average. Soil nitrogen and phosphorous did not vary significantly between years (Brooks 1998). The primary difference in soil nutrients between years was due to differences in amounts of soil water, although soil water content was not directly measured.

The resulting replicated complete blocks design consisted of 5 blocks \times 2 DTNA levels \times 2 topographic positions \times 3 microhabitats \times 4 replicates = 240

sampling stations with repeated samples over 2 years (480 total samples).

Data collection

Each of the 240 sampling stations was sampled once between 15 and 25 April 1994 and a second time between 18 and 26 April 1995 when above-ground live biomass of winter annuals was highest and most species had flowered and begun to set seed. All annual plants were clipped at ground level within a 25×50 cm sampling frame (1250 cm^2), sorted by species, dried to a constant mass at 60°C , and weighed to determine above-ground live dry biomass (0.0001 g precision). Samples collected during the second year were located 20 cm from the first year samples and were considered repeated measures. Although measurement of the seed bank would have produced a more accurate estimate of species richness, measurement of seedling cohorts seemed sufficient because they included forty-four of the forty-nine native annual plant species and all four of the alien annual species known to occur at this site (M. Brooks, unpublished data).

I obtained rainfall data from two United States National Oceanic and Atmospheric Administration (NOAA) weather stations located near the study area. One was located 21 km NW of the study site in Randsburg (59 years of data), the other 40 km SW in Mojave (94 years of data). Linear distance-weighted means of monthly precipitation at these two weather stations were used to estimate current rainfall and long-term average conditions at the DTNA (NOAA 1993, 1994, 1995).

Data analyses

I used analysis of variance (ANOVA) to simultaneously test main and interactive effects of the fixed factors DTNA, Topographic Position, Microhabitat, and Year. To evaluate differences among alien species, I added Species to the ANOVA model as a fixed factor with four levels, one for each alien taxa. When the overall effects were significant, I compared levels within each factor using Fisher's protected least significant difference test (Day and Quinn 1989). In the case of proportional values where sample sizes were unequal, I used the Tukey–Kramer method (Sokal and Rohlf 1995). I used type III sums of squares and effects were considered significant at $P \leq 0.05$.

I analyzed the data as split plots in space and time replicated over five random blocks (Steele and Torrie 1980) using DTNA as the main plot effect, Topographic Position as the subplot effect, Microhabitat as the sub-subplot effect, and Year as the sub-sub-subplot effect. To evaluate the relative effects of different alien species, I added the factor Species as the sub-sub-sub-subplot effect and Year as the sub-sub-sub-sub-subplot effect. A similar model can be found in Steele and Torrie (1980, Table 16.11).

I made calculations manually and using the General Linear Model procedures in SAS version 6.03 (SAS 1988). Prior to using parametric statistics, I inspected the frequency distribution and residuals and generally found them to be non-normal and heteroscedastic. Data were transformed prior to parametric analyses using $\sqrt{(x + 0.5)}$ for absolute species counts, $\log(x + 1)$ for absolute biomass, and $\arcsin(\sqrt{x})$ for proportional species counts and biomass (Sokal and Rohlf 1995). Following transformation, data did not significantly differ from normality (Kolmogorov–Smirnov test $P \leq 0.05$) and variances were homogenous (F_{\max} -test $P > 0.05$). Summary statistics were reported as untransformed averages (± 1 SE).

Results

Over two years I collected 52 annual plant species, five of which were aliens. *Bromus rubens*, *Schismus* spp., and *Erodium cicutarium* were among the top five most abundant species during both years. Seventeen annual plant species were collected during April 1994, three of which were the alien grasses, *Bromus rubens*, *Bromus trinii*, and *Schismus* spp., and one which was the alien forb, *Erodium cicutarium*. Fifty-two species of annual plants were collected during April 1995, including the same alien species collected the previous year plus the alien grass *Bromus tectorum*. Due to a small sample size and large sample variance, *Bromus tectorum* was excluded from individual analyses, but was included in pooled analyses. Hence, four alien species were analyzed individually.

In 1994 alien species richness (species/ 1250 cm^2) ranged from 0 to 4, and averaged $1.03 (\pm 0.07)$ with a median of 1. In 1995 alien species richness also ranged from 0 to 4, but averaged $1.92 (\pm 0.05)$ with a median of 2. In 1994 total biomass (kg/ha) of alien annuals ranged from 0 to 117, and averaged $12 (\pm 1)$ with a median of 2. In 1995 total alien biomass ranged from 0 to 441, and averaged $89 (\pm 7)$ with a median

of 51. Although biomass was directly measured in gm/1250 cm², I reported it in a more standard unit (kg/ha) to facilitate comparison with other studies.

Patterns of habitat invasibility

Habitat invasibility, measured as alien richness, was less strongly associated with the disturbance variable DTNA than with any of the soil nutrient variables including Topographic Position, Microhabitat, and Year (Table 1). The lesser statistical significance of DTNA may have been an artifact of the lesser statistical power of this main plot contrast compared to subordinate plot effects. However, absolute differences between levels of DTNA were much less than between levels of the soil nutrient variables (Figure 3), indicating that alien richness probably did vary least with DTNA.

The spatial soil nutrient variables, Topographic Position and Microhabitat, were significantly associated with alien richness (Table 1), but patterns of richness differed between them (Figure 3). Alien richness was higher in washlets than hummocks during both years, indicating that there were consistently more alien species in the topographic position where soil nutrient levels were highest. In contrast, alien richness was highest beneath creosote bushes during the high rainfall year, and in interspaces during the low rainfall year, representing a highly significant Year \times Microhabitat interaction ($F_{2,32} = 19.54$, $P < 0.001$). There were more alien species in the microhabitats with the highest soil nutrient levels during the year of high rainfall, and in the microhabitat with the lowest nutrient levels during the year of low rainfall.

Table 1. ANOVA results of alien species richness at the DTNA.

Source	df	MS ($\times 10^{-3}$)	F	P
DTNA	1, 4	300	0.38	n.s.
Topographic position	1, 8	14008	5.30	0.049
Microhabitat	2, 32	7556	3.85	0.031
Year	1, 4	91875	65.52	< 0.001
DTNA \times Topographic position	1, 8	133	0.05	n.s.
DTNA \times Microhabitat	2, 32	269	0.14	n.s.
DTNA \times Year	1, 4	133	0.24	n.s.
Residual	470	798		

n.s. = not significant at $P < 0.05$.

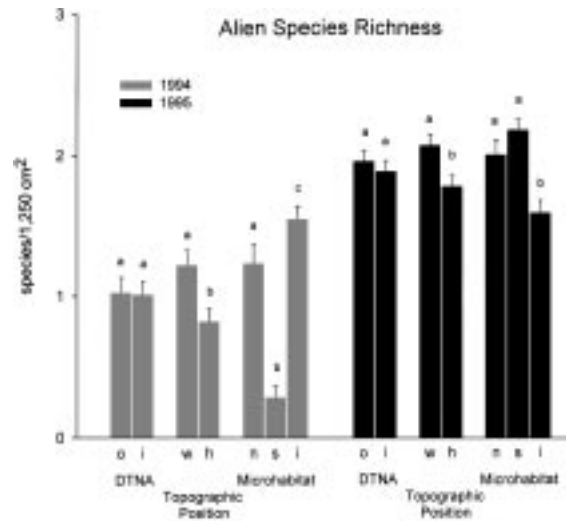


Figure 3. Alien species richness in April 1994 and 1995 at the DTNA. Data is presented for three factors, DTNA (inside = i, outside = o), topographic position (washlet = w, hummock = h), and microhabitat (*Larrea*-north = n, *Larrea*-south = s, interspace = i). Dissimilar letters above the bars indicate significant differences within each factor using Fisher's protected LSD ($P < 0.05$). Vertical bars represent one SE.

The temporal soil nutrient variable, Year, was also strongly associated with alien richness (Table 1), but the patterns differed for absolute and proportional measures (Figure 4). As predicted, absolute alien richness was lower during 1994 when rainfall was low than 1995 when rainfall was high, but the pattern for proportional alien richness was opposite. Proportional alien richness was higher during the year of low rainfall because few native species germinated and grew to seedlings, whereas proportional alien richness was lower during the year of high rainfall because many native species germinated and grew to seedlings.

Patterns of alien dominance

Alien dominance, measured as total alien biomass, displayed similar but more significant patterns as alien richness. Alien biomass was not significantly associated with DTNA, but was with Topographic Position, Microhabitat, and Year (Table 2). Although the effect of DTNA was not significant over the two years, alien biomass was significantly higher outside than inside the DTNA during 1994 (Figure 5). As observed for alien richness, alien biomass was higher in washlets than hummocks, and highest beneath creosote bushes

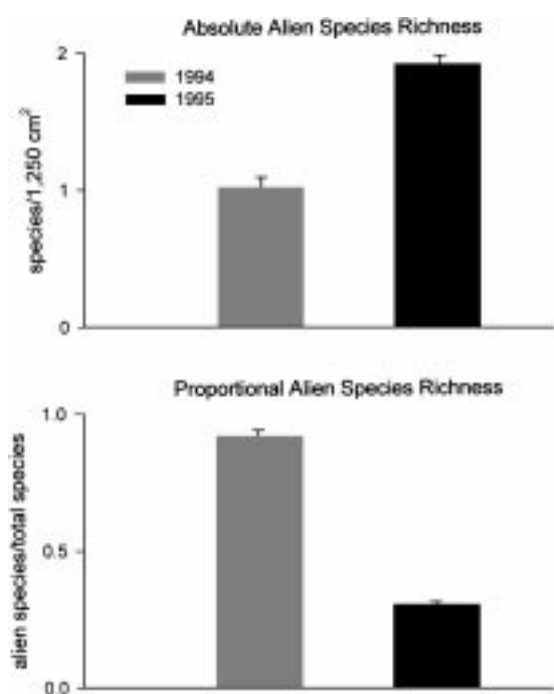


Figure 4. Alien species richness in April 1994 and 1995 pooled over all levels of disturbance, topographic position, and microhabitat at the DTNA. All contrasts within absolute and proportional alien richness are significant using Fisher's protected LSD for absolute values, and the Tukey-Kramer procedure for proportional values ($P < 0.05$). Vertical bars represent one SE.

Table 2. ANOVA results of alien biomass at the DTNA.

Source	df	MS	F	P
DTNA	1, 4	1228	0.46	n.s.
Topographic position	1, 8	73624	24.05	< 0.001
Microhabitat	2, 32	137974	7.90	0.001
Year	1, 4	712159	214.59	< 0.001
DTNA × Topographic position	1, 8	8500	2.78	n.s.
DTNA × Microhabitat	2, 32	18811	1.08	n.s.
DTNA × Year	1, 4	199	0.11	n.s.
Residual	470	4472		

n.s. = not significant at $P < 0.05$.

during the high rainfall year, and in interspaces during the low rainfall year. Temporal patterns of alien biomass were also similar to those of alien richness, with higher absolute values during 1995, but higher proportional values during the 1994 (Figure 6). Thus, where and when alien species were most numerous, alien biomass was highest.

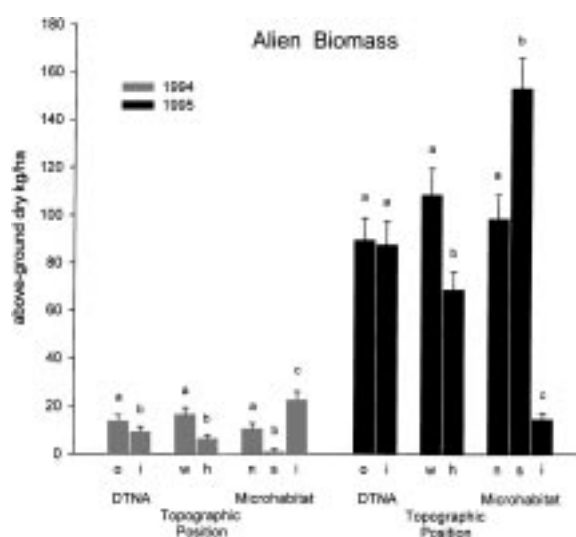


Figure 5. Total alien biomass in April 1994 and 1995 at the DTNA. Data is presented for three factors, DTNA (inside = i, outside = o), topographic position (washlet = w, hummock = h), and microhabitat (*Larrea*-north = n, *Larrea*-south = s, interspace = i). Dissimilar letters above the bars indicate significant differences within each factor using Fisher's protected LSD ($P < 0.05$). Vertical bars represent one SE.

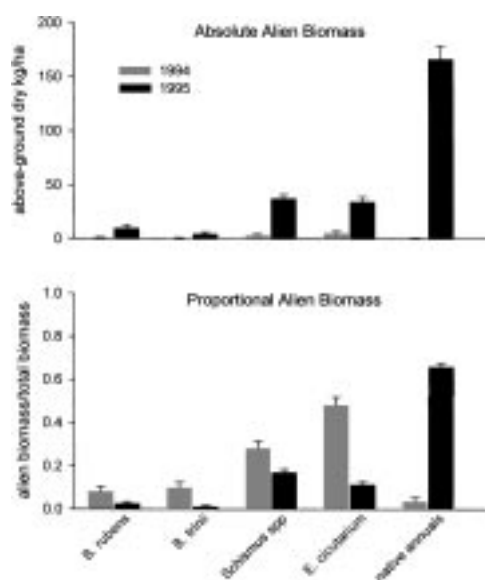


Figure 6. Alien biomass in April 1994 and 1995 pooled over all levels of disturbance, topographic position, and microhabitat at the DTNA. All contrasts within absolute and proportional alien richness are significant using Fisher's protected LSD for absolute values, and the Tukey-Kramer procedure for proportional values ($P < 0.05$). Vertical bars represent one SE.

Variations among alien species

Many of the patterns observed for total alien biomass were more precisely attributed to one or two alien species. This large variation among alien species was reflected by the highly significant species factor that accounted for 70% of the mean-square variation in absolute alien biomass in the full ANOVA model ($F_{3,144} = 23.67, P < 0.001$).

Individual alien species displayed differing associations with DTNA, and in some cases these associations

varied among years. For example, biomass of *Schismus* spp. was higher outside than inside the DTNA during 1994, whereas biomass of *Bromus rubens* was higher outside the DTNA in 1995 (Figure 7). *Schismus* spp. was the only alien to display a significant effect of DTNA over both years ($F_{1,4} = 14.73, P = 0.019$). Biomasses of *Bromus trinius* and *Erodium cicutarium* were not significantly associated with DTNA within either year (Figure 7).

The strong positive association of total alien biomass with washlets was due primarily to high biomass of

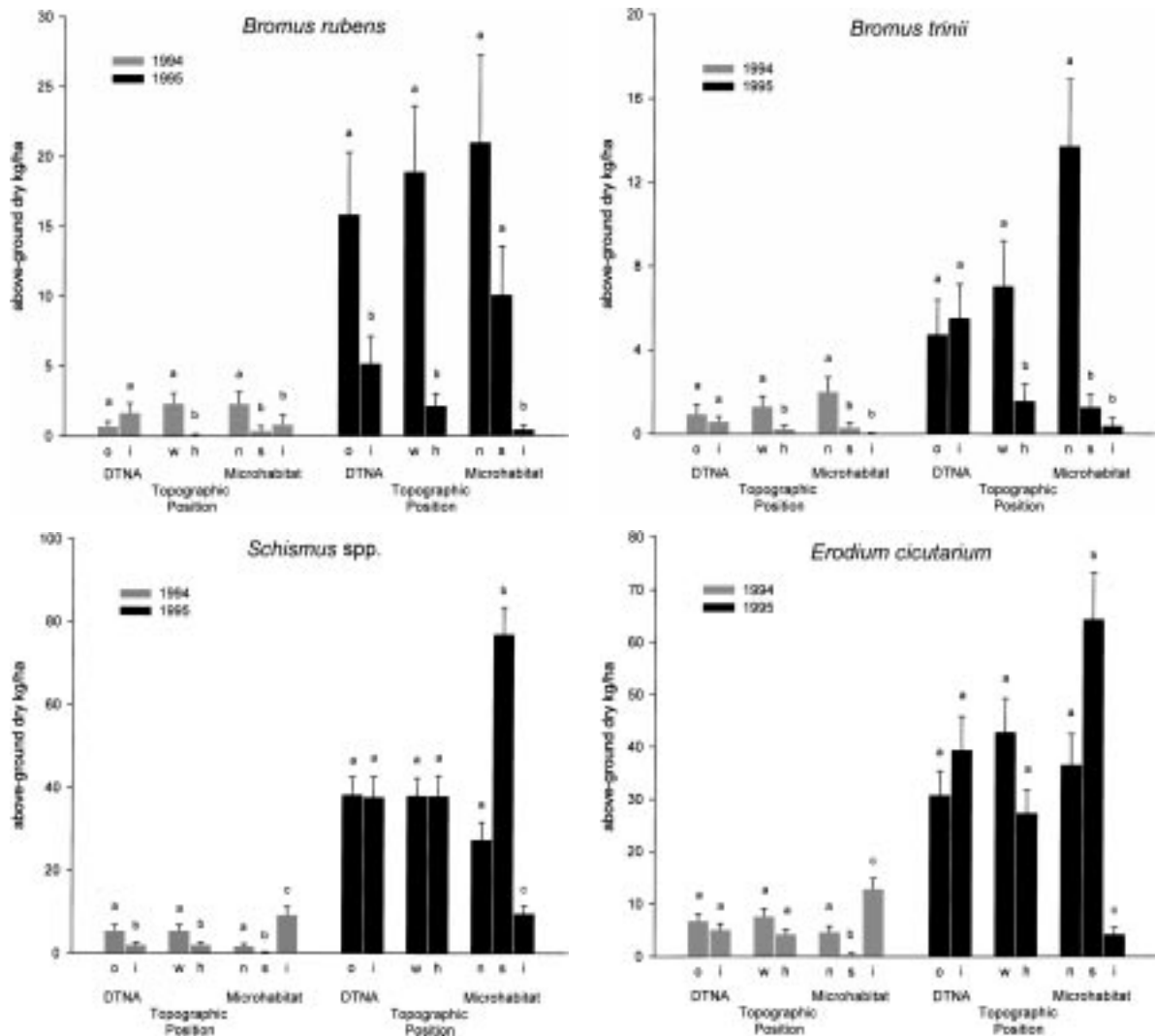


Figure 7. Biomass of individual alien annual plants in April 1994 and 1995 at the DTNA. Data is presented for three factors, DTNA (inside = i, outside = o), topographic position (washlet = w, hummock = h), and microhabitat (*Larrea*-north = n, *Larrea*-south = s, interspace = i). Dissimilar letters above the bars indicate significant differences within each factor using Fisher's protected LSD for absolute values ($P < 0.05$). Vertical bars represent one SE.

Bromus rubens ($F_{1,8} = 12.43$, $P = 0.008$) and *Bromus trinitii* ($F_{1,8} = 11.30$, $P = 0.010$) over both years and within years (Figure 7). Biomass of the other aliens were also generally higher in washlets than hummocks, but the differences were not significant over both years for *Schismus* spp. ($F_{1,8} = 2.59$, $P = 0.145$) or *Erodium cicutarium* ($F_{1,8} = 3.23$, $P = 0.109$).

The most dramatic differences between years occurred among levels of Microhabitat. Over both years biomass of *Bromus trinitii* ($F_{2,32} = 4.31$, $P = 0.022$), but not *Bromus rubens* ($F_{2,32} = 2.34$, $P = 0.113$), was significantly higher under creosote bushes, although both were higher under creosote bushes within years (Figure 7). Biomasses of *Schismus* spp. and *Erodium cicutarium* were not significantly affected by Microhabitat over both years ($F_{2,32} = 0.22$, $P = 0.804$; $F_{2,32} = 2.16$, $P = 0.129$), primarily because their spatial patterns differed so strongly between years (Year \times Microhabitat; $F_{2,32} = 44.26$, $P < 0.001$; $F_{2,32} = 22.99$, $P < 0.001$). Their biomasses were higher in interspaces during 1994 and in *Larrea*-south during 1995 (Figure 7). Clearly, the association of alien biomass with Microhabitat depended on the year and species being analyzed.

A significant Year \times Species interaction for absolute and proportional biomass indicated that alien species differed in their responses to Year ($F_{3,144} = 31.56$, $P < 0.001$). Absolute biomasses of *Bromus rubens* and *Bromus trinitii* did not vary as much among years as *Schismus* spp. and *Erodium cicutarium*, and none of the aliens varied nearly as much as native annuals (Figure 6). Proportional biomasses of all four alien species were higher in the year of low than in the year of high rainfall.

Discussion

Spatial and temporal patterns of alien richness and total alien biomass were similar, indicating that invasibility and alien dominance were positively associated in this study. No single alien species dominated any one place in space or time, and four of five alien species contributed significantly to total alien biomass. Three of these alien species, *Bromus rubens*, *Schismus* spp., and *Erodium cicutarium*, dominate annual plant biomass in most parts of the Mojave Desert (Brooks 1998), although the invasibility of this desert is relatively low, where aliens comprise 9% (Rowlands et al. 1982) to 11% of the total flora (J. Haley, personal

communication). This pattern of high alien annual plant dominance and low alien species richness is consistent among sites in the central, southern, and western regions of this desert (Brooks 1998). In plant communities with more total alien species and a smaller percentage comprising the majority of annual plant biomass, patterns of invasibility and dominance may differ. In addition, the 1250 cm² sampling scale used in this study was the largest feasible for comparing microhabitats, but larger spatial scales were possible for comparing topographic positions, disturbance levels, and years. To test the generality of the results, habitat invasibility and alien dominance need to be compared among plant communities containing varied numbers of alien species with varied proportions comprising their total alien biomass and at other spatial scales.

The smaller variation of alien dominance due to disturbance than soil nutrients may have been due to differing ranges in variation within each that resulted in differing powers of detecting significant effects. The two levels of disturbance were the result of only 15 years of differing sheep grazing and OHV use, and the contrast between these levels may not have been as high as the contrast between soil nutrient levels. Considering that ecological succession is either non-existent (Muller 1940; Shreve 1942) or operates at the scale of centuries in the Mojave Desert (Wells 1961; Vasek 1983; Webb et al. 1987), little difference in plant community composition may occur after only 15 years. With greater variation among levels and types of disturbance, its effect on species richness and biomass of aliens may be more apparent. Furthermore, there are many areas in this desert with much higher levels of disturbance than those found at the DTNA. Areas such as livestock watering sites, OHV camping sites, transportation corridors, and urbanized landscapes appear to be highly invasible and dominated by alien plants (M. Brooks, personal observation), but only limited quantitative data exist from the Mojave Desert (Brooks 1998). Hence, the significance of disturbance may be greater at higher levels, but this hypothesis remains to be tested in this desert.

Combined effects of disturbance and soil nutrients on habitat invasibility were not detected in this study. As mentioned in the Introduction, even the most productive microsites in the Mojave Desert are relatively unproductive compared to other ecosystems. The range of soil nutrient levels in this study did not seem to include the high levels at which Huston (1994) predicted this interaction should occur.

High richness and biomass of aliens in washlets suggests that run-on areas may facilitate the spread of aliens through an otherwise inhospitable landscape. Because this effect was significant during two years of contrasting rainfall, it appears that run-on areas could act as refugia for aliens allowing them to persist through droughts. An extensive review of the ecology and management of plant invasions in semi-arid southern Africa indicates that conditions in washes are conducive to the growth of alien species and can promote their spread (MacDonald et al. 1986). The corridor structure of riparian zones can facilitate plant dispersal into adjacent upland areas (Forman and Godron 1986). By providing locally high levels of soil moisture, washes and washlets may serve as conduits for the flow of aliens from more mesic regions into the more arid Mojave Desert.

Associations of annual plant species with perennial shrubs have been extensively documented in the deserts of North America (Shreve 1931; Went 1942; Muller 1953; Adams et al. 1970; Halvorson and Patten 1975; Shmida and Whittaker 1981; Samson 1986) and elsewhere (Zohary 1973; Keeley and Johnson 1977; Noy-Meir 1979). The current study suggests that *Bromus rubens* and *Bromus trinii* are strongly associated with creosote bushes, whereas dominance of *Schismus* spp. and *Erodium cicutarium* varies among microhabitats during years of contrasting rainfall. Varying amounts of microhabitat affinities among years were also found for annual plants in the central Mojave Desert where biomass patterns of *Bromus rubens*, *Schismus* spp., and *Erodium cicutarium* were similar to those in the current study (Samson 1986), and in the Sinai Desert of Israel (Tielbörger and Kadmon 1997). Thus, responses of alien plants to microhabitats of contrasting soil nutrient levels can vary among species.

Differences in alien species richness and biomass among topographic positions and microhabitats could have been due partly to the differential accumulation of seeds in washlets compared to hummocks and beneath creosote bushes compared to interspaces. However, the seeds of these species do not seem to be predisposed to accumulating in any particular topographic position or microhabitat, because they are generally adapted for dispersal by animals which deposit them in a wide variety of locations (M. Brooks, personal observation). In addition, patterns of absolute alien dominance observed in this study were similar to those of proportional alien dominance reported from these same data (Brooks 1998), indicating that aliens were proportionally more productive in washlets than hummocks

and beneath creosote bushes than interspaces. Experimental addition of nitrogen and phosphorous increased the biomass of *Bromus rubens*, *Schismus* spp., and *Erodium cicutarium* (Brooks 1998), and soil enriched with available nitrogen after fire is typically dominated by *Bromus rubens* in the Mojave Desert (M. Brooks, unpublished data). These data indicate that soil nutrients are likely a primary factor limiting the productivity of alien annual plants in the Mojave Desert.

As predicted, absolute biomass of aliens was higher during the high than the low rainfall year, but the opposite was observed for proportional alien biomass. This difference was likely due to the contrasting germination requirements of alien and native annuals. Natives only germinate in large numbers after relatively large rainfall events (Beatley 1974; Venable and Lawlor 1980), whereas aliens require far less rainfall to germinate (Beatley 1966). In the Chilean Desert alien annual plants required only 10 mm of rainfall to germinate whereas native species typically needed ≤ 40 mm (Vidiella and Armesto 1989), and *Schismus arabicus* germinated after only 5 mm of rainfall (Gutierrez 1992). Similar observations have been made in the Mojave Desert (M. Brooks, personal observation). Compared to natives, the germination fraction of alien annuals apparently does not vary much among years, and proportional alien biomass should be highest during dry years when native annual seedlings are relatively scarce. Germination during years of low rainfall may reduce population levels of aliens if their seedlings die from water stress before reproducing. Aliens may be able to persist in the Mojave Desert due to their superior colonizing abilities that allow them to recolonize areas during years of above-average rainfall. Hunter (1991) showed that *Bromus rubens* became dominant at a site in the northern Mojave Desert during a relatively wet rainfall cycle that lasted fifteen years. It is unknown if prolonged drought could reverse this trend, but it seems possible that losses to alien seed banks during dry years may lead to crashes in local populations (F. Vasek, personal communication).

Positive associations with high soil nutrient levels were more consistent for *Bromus rubens* and *Bromus trinii*, two species that originated from relatively mesic and semi-arid Mediterranean climatic regions (Jackson 1985; Brooks 2000b). These species may not be well adapted to the semi-arid to arid climate in the Mojave Desert, which may explain why they experience local population crashes after droughts (M. Brooks, personal observation). In contrast, *Erodium cicutarium* and especially *Schismus* spp. (Brooks 2000a)

originated from more arid regions, and may be better adapted for the low resource levels characteristic of the Mojave Desert. A predisposition for arid conditions may explain why these species were able to successfully establish populations in harsh interspaces, and spread throughout the Mojave Desert (Kemp and Brooks 1998).

Schismus spp. in particular seems well adapted for arid ecosystems. In the Negev Desert, *Schismus arabicus* plants produce an average of 10 seeds during dry years and up to 100 seeds during wet years (Loria and Noy-Meir 1979–1980). In the Sonoran Desert *Schismus barbatus* can maintain a substantial seed bank that may help it survive prolonged droughts (Venable et al. 1993). Although disturbance and soil nutrient status were positively associated with alien richness and biomass at this site, other factors such as the life history characteristics of potential invaders should be considered when evaluating habitat invasibility and potential alien dominance in the Mojave Desert.

This study showed that soil nutrients can be more important than disturbance in promoting habitat invasibility and dominance by alien annual plants in the Mojave Desert, but it is unknown if this pattern is widespread. Soil nutrients and disturbance appear to be important habitat factors that influence plant invasions, but their effects need to be studied more extensively in this desert to develop reliable models of habitat invasibility and alien dominance. With increased human populations and changing global weather patterns atmospheric nitrogen deposition and rainfall may increase in the Mojave Desert, which could further facilitate annual plant invasions and promote annual plant dominance in this region. The results of this study suggest that monitoring for the arrival of new aliens should focus on regions with high levels of rainfall and soil nutrients, and on washes and beneath-canopy microhabitats. The search for new annual plant invaders and the evaluation of the geographic range of existing species should be done during years of high rainfall when annual plant productivity is high and alien species are easy to locate. The potential ecological ranges of each alien species should be evaluated separately, because the characteristics of individual species can differ significantly.

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