

# Dominance and environmental correlates of alien annual plants in the Mojave Desert, USA

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## Abstract

Land managers are concerned about the negative effects of alien annual plants on native plants, threatened and endangered species such as the desert tortoise (*Gopherus agassizii*), and ecosystem integrity in the Mojave Desert. Management of alien plants is hampered by a lack of information regarding the dominance and environmental correlates of these species. The results of this study indicate that alien plant species comprised a small fraction of the total annual plant flora, but most of the annual plant community biomass. When rainfall was high in 1995, aliens comprised 6% of the flora and 66% of the biomass. When rainfall was low in 1999, aliens comprised 27% of the flora and 91% of the biomass. *Bromus rubens*, *Schismus* spp. (*S. arabicus* and *S. barbatus*), and *Erodium cicutarium* were the predominant alien species during both years, comprising 99% of the alien biomass. *B. rubens* was more abundant in relatively mesic microhabitats beneath shrub canopies and at higher elevations above 800–1000 m, whereas *Schismus* spp. and *E. cicutarium* were more abundant in the relatively arid interspaces between shrubs, and, for *Schismus* spp., at lower elevations as well. Disturbance variables were more reliable indicators of alien dominance than were productivity or native plant diversity variables, although relationships often varied between years of contrasting rainfall. The strongest environmental correlates occurred between dirt road density and alien species richness and biomass of *E. cicutarium*, and between frequency and size of fires and biomass of *B. rubens*.

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## 1. Introduction

Alien annual plants pose major threats to the integrity of ecosystems and to a wide range of plant and animal species in the Mojave Desert. The effects of alien species on federally threatened and endangered species such as the desert tortoise (*Gopherus agassizii*) are of particular concern to the United States (US) Fish and Wildlife Service (FWS) and land management agencies (FWS, 1994; Brooks and Esque, 2002). One negative effect on recovery efforts for the desert tortoise stems from decreased amounts and altered seasonal availabilities of preferred food plants (FWS, 1994). This threat is based on the reduced biomass and diversity of native annual plants that can result from competition with alien annual plants (Brooks, 2000a), and the potential dependency of desert tortoises on native annuals which can comprise 95% of their diet (Jennings, 1993, 2002; Oftedal et al., 2002). Alien annual grasses also contribute to increased frequency of fires (Brooks, 1999a; Brooks and Pyke, 2001; Brooks and Esque, 2002; Brooks and Minnich, 2006), which can directly kill desert tortoises (Woodbury and Hardy, 1948; Homer et al., 1998; Esque et al., 2003), alter the structure of their habitat, and initiate a wide range of ecosystem changes including altered fire regimes (D'Antonio and Vitousek, 1992; Brooks et al., 2004). Land managers have a mandate to recover the desert tortoise and its habitat (FWS, 1994; Berry, 1997), but these goals are hampered by a lack of basic information regarding the relative dominance and environmental correlates of alien annual plants.

Global patterns of alien plant dominance provide indications of environmental conditions that may be associated with alien annual plant abundance in the Mojave Desert. Alien species richness is often positively correlated with high levels of disturbance (Elton, 1958; Grime, 1979; Hobbs, 1989), intermediate levels of plant productivity (Grime, 1979; Rejmánek, 1989; Hobbs and Huenneke, 1992), and low levels of plant diversity (Elton, 1958). However, the relative importance of each factor remains unclear and likely varies among ecosystems. At one site in the Mojave Desert, alien richness and biomass were positively associated with microhabitats containing locally high levels of soil nutrients, moisture, and, to a lesser extent, disturbance (Brooks, 1999b). It is unknown if the localized patterns observed by Brooks (1999b) apply at larger landscape scales in the Mojave Desert.

Disturbances such as livestock grazing, off-highway vehicle (OHV) use, fire, urbanization, roads, and agriculture appear to be positively associated with species richness and biomass of alien plants in the Mojave Desert. A few empirical studies demonstrate these associations. Alien annuals had high density, biomass, or cover near roads (Frenkel, 1977; Johnson et al., 1975), in an area of OHV use compared to an area where OHV use was lower (Davidson and Fox, 1974), in an area where both OHV use and grazing were present compared to an area where both disturbances had been excluded for at least 10 years (Brooks, 1995, 1999b), in two grazed areas compared with ungrazed areas (Webb and Stielstra, 1979), and in areas near livestock watering sites (Brooks et al., 2006). Alien annual grasses promote fires worldwide (D'Antonio and Vitousek, 1992; Brooks et al., 2004) and in the Mojave Desert (Brooks, 1999a; Brooks and Pyke, 2001; Brooks and Esque 2002; Brooks and Minnich, 2006). Repeated fires favor alien annual grasses over native perennial species in arid and semi-arid regions of south-western North America (Zedler et al., 1983; Brown and Minnich, 1986; Brooks and Pyke, 2001; Brooks and Minnich, 2006). These studies indicate that species richness and biomass of alien annual plants are positively correlated with disturbance, but it is unknown which disturbance

variables have the greatest effect or how the effects of disturbance compare to the effects of productivity and native plant diversity.

Productivity may be positively correlated with species richness and biomass of alien plants in the Mojave Desert, in contrast to many other ecosystems where alien dominance peaks at intermediate levels of productivity (Huston, 1994). Productivity is often measured as plant biomass (Begon et al., 1996), and soil water and nitrogen are especially good estimates of productivity in the Mojave Desert (Rundel and Gibson, 1996). Plant biomass and soil nutrient levels are relatively low in the Mojave Desert compared to other ecosystems (Rundel and Gibson, 1996). Thus, they may not reach the high productivity levels that can hinder plant invasions. In addition, the dominance of alien annual plants can increase with increasing soil nutrient levels in the Mojave Desert (Brooks, 1999b, 2003).

Diversity of native annual and perennial plants may have differing effects on aliens. Natives may interact with alien annual plants through direct, indirect, or apparent competition (Goldberg and Scheiner, 1993). Low diversity of native annuals may be positively correlated with alien richness if there is unfilled niche space for aliens to invade or if invading aliens reduce native diversity by competitive exclusion. In contrast, perennial native plants can interact with aliens either through competition (Eissenstat and Caldwell, 1988; Melgoza et al., 1990; Melgoza and Nowak, 1991) or by creating variation in environmental factors such as ambient light and soil temperature, moisture, mineral nutrients, texture, and depth (Brooks, 1999b). Diversity of native perennials or density of individual perennial species also may be negatively correlated with alien richness and biomass due to competition or other factors (Holzapfel and Mahall, 1999), or positively correlated with aliens if high diversity of native perennials provides increased spatial habitat heterogeneity and niche space. Thus, it is unclear if consistent relationships exist between native plant diversity and alien annual plants.

In this paper we documented the biomass dominance of alien annual plants and their environmental correlates during 2 years of contrasting rainfall in the Mojave Desert. We tested the hypotheses that species richness and biomass of alien annual plants would be high where disturbance or productivity was high, and that alien richness and biomass would be correlated with native plant diversity, either positively or negatively. We determined the effects of geographic variation on these hypotheses by evaluating elevation, latitude, and longitude as covariates. The results of this study provide important new information on the dominance of alien annual plants in the Mojave Desert.

## 2. Materials and methods

### 2.1. Study area

We focused on public lands under the jurisdiction of the Department of the Interior, Bureau of Land Management (BLM), and designated as Desert Wildlife Management Areas (DWMAs) and critical habitat for the federally threatened desert tortoise (FWS, 1990, 1994). DWMAs and critical habitat represent some of the least disturbed lands remaining in the Mojave and Colorado deserts of California, Nevada, and Utah (Berry, 1997). Although disturbance levels were relatively low, many of these areas have experienced as much as 125 years of historical and recent impacts from mining, livestock grazing, roads, utility lines, and other anthropogenic uses (Norris and Carrico, 1978;

BLM, 1980; Lovich and Bainbridge, 1999). We studied the Superior-Cronese, Ord-Rodman, and Fremont-Kramer DWMA, which represented the central, southern, and western Mojave Desert (Fig. 1) (regional distinctions adapted from Rowlands et al., 1982).

## 2.2. Sampling design

Public lands within the Mojave Desert are delineated using a cadastral survey system of townships (36 mi<sup>2</sup>, 129.24 km<sup>2</sup>) and township sections (1 mi<sup>2</sup>, 2.59 km<sup>2</sup>). We randomly chose half the townships located within each of the three DWMA for sampling: 10 townships in the Fremont-Kramer DWMA; 8 in the Ord-Rodman DWMA; and 16 in the Superior-Cronese DWMA (Fig. 1). Within each of the 34 townships, a township section was randomly chosen from those that did not contain playas, mountaintops, or private lands. Within each section, a study site was chosen that was accessible to field crews and was greater than 50 m from dirt roads, 2 km from paved roads, and 2 km from human habitations. These sites averaged 886 m elevation, ranging from 683 to 1402 m. The entire site selection process was done in the lab using US Geological Survey (USGS) 7.5'' topographic maps.

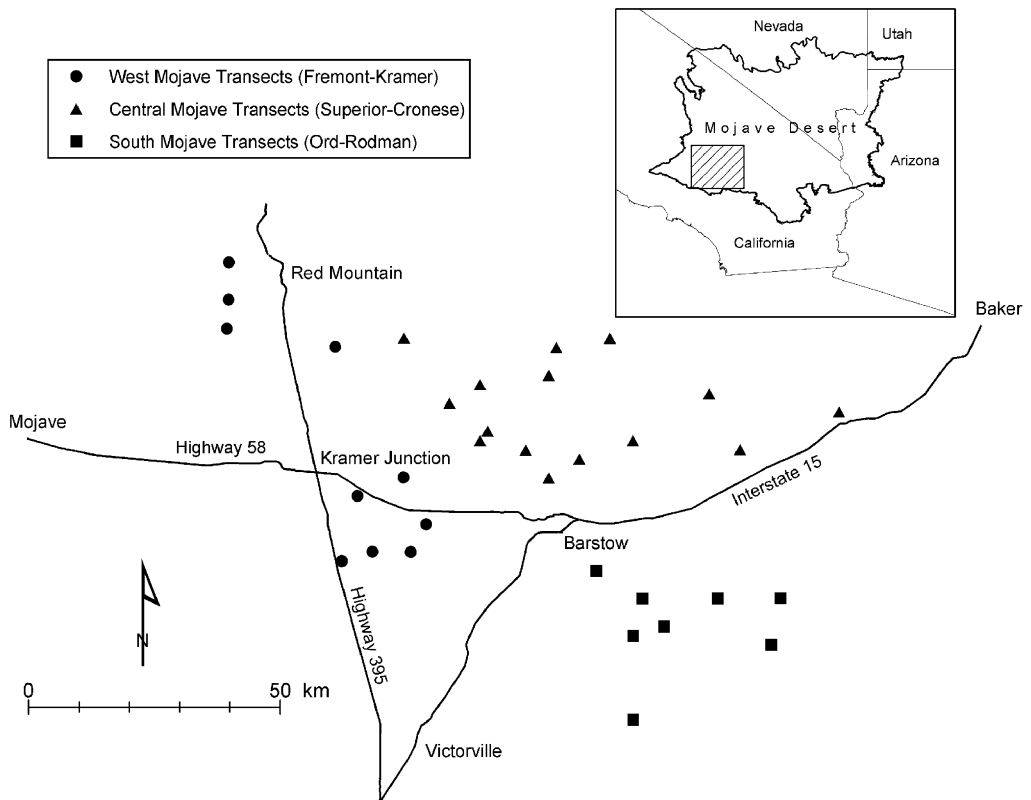


Fig. 1. Study sites in the central (16 sites), southern (8 sites), and western (10 sites) Mojave Desert, California, USA.

At each site we established a single 360 m linear transect parallel to the elevational contour with 25 sampling points placed 15 m apart. At each sampling point, we located the nearest woody shrub, bunchgrass, or cactus with a maximum canopy diameter > 50 cm and placed a 10 × 20 cm sampling frame in each of two microhabitats near the plant: (1) beneath the north side of its canopy (beneath-canopy); and (2) in the interspace located adjacent to, but > 1 m from, its canopy edge or that of any other perennial plant (interspace) (34 sites × 25 transect points × 2 microhabitats = 1700 sampling frames). In the beneath-canopy microhabitat the sampling frame was oriented with its short axis perpendicular to the base of the shrub, and in the interspace microhabitat the sampling frame was oriented randomly by dropping it to the ground from a height of 2 m.

Sampling was stratified at each site between the beneath-canopy and interspace microhabitats to account for local variation in annual plant community composition (Shreve, 1931; Muller, 1953; Samson, 1986). If sampling was completely random at each site, 6% (3 of 50) of the samples would have occurred in the beneath-canopy microhabitat compared to 94% (47 of 50) in the interspace microhabitat, because perennial cover averaged 6% over the 34 sites. Thus, alien species that primarily occurred under shrubs would have been greatly undersampled.

We sampled annual plants in spring 1995 and 1999 to compare the habitat associations of alien annual plants and the composition of seedling cohorts during years of contrasting rainfall. We used rainfall data recorded at weather stations operated by the National Oceanographic and Atmospheric Administration (NOAA). Prior to spring 1995, winter rainfall (Nov–Apr) was 200% of the long-term average for the region (NOAA, 1994, 1995). Prior to spring 1999, winter rainfall was 48% of the regional average (NOAA, 1998, 1999). This study was also preceded by an approximately 20 years period of above-average rainfall in the Mojave Desert (Hereford et al., 2006).

Annual plants were sampled near peak biomass (Jennings, 2001) from 12 April to 11 May 1995, and 20 March to 11 April 1999. Live plants rooted within each sampling frame were clipped at ground-level, dried to a constant mass at 60 °C, and weighed to determine dry above-ground live biomass. Samples in 1999 were collected 10 cm from where they were collected in 1995.

### 2.3. *Predictor variables and covariates*

Disturbance was estimated using nine variables: (1) sheep grazing intensity; (2) cattle grazing intensity; (3) OHV intensity; (4) fire frequency; (5) area burned; (6) dirt road dominance; (7) paved road proximity; (8) urban area proximity; and (9) agricultural area proximity. Intensity of livestock grazing was defined as presence or absence of cattle or sheep based on grazing allotments managed by the BLM (BLM, 1980, as amended). Intensity of OHV use was estimated as low, moderate, or high based upon on-site evidence of use, such as trails and camping areas, as well as BLM records of land use from 1960 through 1990. Incomplete historical records prevented more precise measurements of grazing and OHV histories. Fire frequency and area burned were calculated within the surrounding 79 km<sup>2</sup> (5 km radius) of each site using BLM fire records (DI-1202 reports) from 1980 to 1994, inclusive. Although none of the sampling transects passed through areas with evidence of previous burning (e.g. charred stems or stumps), some were as close as 100 m to previously burned areas. Dominance of dirt roads was measured as their total length (km) in the township section within which the site was located, using USGS 7.5''

topographic maps. Proximity to paved roads, urban areas, and agricultural areas was defined as  $1/\text{distance}$ , such that increasing values represented increasing proximity to these sources of disturbance. Distances were determined using USGS, BLM, and Department of Defense maps, reports, land use plans, and other records.

Productivity was estimated using four variables: (1) annual rainfall; (2) total soil nitrogen; (3) native annual plant biomass; and (4) perennial plant cover. Long-term average annual rainfall was determined using NOAA rainfall records from weather stations located at Barstow, Daggett, Mojave, Palmdale, Randsburg, and Victorville, California (NOAA, 1994, 1995). At each site, linear distance-weighted averages from the closest three weather stations were used to determine average annual rainfall. Winter rainfall (Nov–April) and winter:summer rainfall were also measured, but were not included in the analyses because they were both highly correlated with annual rainfall ( $r > 0.96$ ). Total Kjeldahl nitrogen was measured from 8 cm diameter  $\times$  7 cm deep soil cores collected at each of the 1700 sampling stations during June 1995. Soil analyses were performed by the University of California, Davis, Division of Agriculture and Natural Resources Analytical Laboratory. Biomass of native annual grasses and forbs was concurrently measured with alien plant biomass during 1995 and 1999. Perennial plant cover was estimated by point-quarter analysis of the 25 sampling points at each site during June 1995 (Greig-Smith, 1964).

Native plant diversity was estimated using two variables: (1) annual plant diversity; and (2) perennial plant diversity. For annual plants, the numbers of native species rooted within each  $10 \times 20$  cm sampling station were recorded. For perennials, the numbers of native species were counted by point-quarter analysis at each of the 25 sampling points on each transect. Diversity was calculated using the Shannon-Weiner index ( $H'$ ) (Pielou, 1966), which was strongly correlated with richness and evenness ( $r > 0.90$ ).

The three covariates included: (1) elevation; (2) latitude; and (3) longitude. These values were measured and verified for each of the 34 study sites using USGS 7.5" topographic maps and a global positioning system (GPS) navigation unit.

#### 2.4. Statistical analyses

The response variables were species richness of alien annual plants, biomass of alien annuals, biomass of alien annual grasses, biomass of *Bromus madritensis* subsp. *rubens* (hereafter called *B. rubens*), biomass of *Erodium cicutarium*, and the combined biomass of *Schismus arabicus* and *S. barbatus* (hereafter called *Schismus* spp.). The two species of *Schismus* were combined because they could not be reliably differentiated in the field. Final landscape averages for each response variable at each site were calculated by weighting the raw data from the beneath-canopy microhabitat by the percent cover of perennial plants (range 1–17% among sites), and from the interspace microhabitat by the average cover of interspace (range 83–99%). This ensured equal sampling of the two microhabitat extremes, while not biasing the final values for each site toward the beneath-canopy data. Residuals of the response variables were generally non-normal and heteroscedastic. Hence, response variables were transformed prior to analysis using  $\sqrt{(x+0.5)}$  for species richness and  $\log(x+1)$  for biomass (Sokal and Rohlf, 1995). Following transformation, data were normally distributed (Kolmogorov–Smirnov test,  $p \leq 0.05$ ) and non-heteroscedastic ( $F_{\max}$  test,  $p > 0.20$ ).

The predictor variables included measures of disturbance, productivity, and native plant diversity. We used principal component analysis (PCA) with varimax rotation (SAS, 1988) to produce a reduced set of uncorrelated predictor variables within the disturbance and productivity categories (Table 1). Because the precision and units of measurement within each category varied, we performed the PCA on the correlation matrix of the raw data (Jackson, 2003). Within the disturbance and productivity categories, we chose a subset of PCA variables that cumulatively explained >75% of the variation in the raw data, was located to the left of the first inflection point on the scree plot, and had eigenvalues > 1.00 (Jackson, 2003). In all cases, these subsets were also chosen by the broken-stick method, a method of PCA variable selection that is highly consistent among data sets with varied

Table 1  
Principal components analysis of predictor variables showing factor loading  $\geq 0.50$  in bold type

|  | Rotated factor loadings |             |             |             |             |             |
|--|-------------------------|-------------|-------------|-------------|-------------|-------------|
|  | PC1                     | PC2         | PC3         | PC4         | PC5         | PC6         |
| Disturbance  | URBAN                   | FIRE        | CATTLE      | AGRI        | OHVS        | DIRTROAD    |
| Proximity to nearest agricultural area             | 0.16                    | -0.04       | 0.10        | <b>0.91</b> | -0.16       | -0.10       |
| Proximity to nearest small town or urban area      | <b>0.86</b>             | 0.13        | 0.14        | 0.18        | 0.02        | 0.16        |
| Area burned within 5 km from 1980 to 1994          | 0.29                    | <b>0.82</b> | -0.12       | 0.05        | -0.10       | -0.18       |
| Number of fires within 5k from 1980 to 1994        | -0.11                   | <b>0.92</b> | 0.07        | -0.11       | -0.05       | 0.01        |
| Located in an ephemeral sheep grazing allotment    | -0.36                   | -0.14       | -0.43       | <b>0.50</b> | 0.42        | 0.24        |
| Located in a perennial cattle grazing allotment    | 0.08                    | -0.05       | <b>0.96</b> | 0.07        | -0.02       | 0.07        |
| History of OHV disturbance                         | -0.04                   | -0.10       | -0.02       | -0.13       | <b>0.96</b> | -0.03       |
| Total length of dirt roads in the township section | 0.07                    | -0.11       | 0.05        | -0.06       | -0.01       | <b>0.97</b> |
| Proximity to nearest paved road                    | 0.93                    | -0.02       | 0.01        | -0.04       | -0.11       | -0.06       |
| Proportion of variance explained                   | 0.21                    | 0.18        | 0.13        | 0.13        | 0.13        | 0.12        |
| Plant productivity                                 | RAIN                    | NATIVEBIOM  | NITR        |             |             |             |
| Total soil nitrogen                                | -0.02                   | 0.08        | <b>0.99</b> |             |             |             |
| Average annual rainfall                            | <b>0.91</b>             | 0.10        | 0.04        |             |             |             |
| Absolute biomass of native annual plants           | 0.04                    | <b>0.93</b> | 0.06        |             |             |             |
| Percent cover of perennial shrubs and bunchgrasses | <b>-0.62</b>            | <b>0.53</b> | 0.15        |             |             |             |
| Proportion of variance explained                   | 0.30                    | 0.29        | 0.25        |             |             |             |

correlation structures. This reduced the number of disturbance and productivity variables, and produced an uncorrelated subset of each that was similar in variance and contained >75% of the raw data variation.

Variance among disturbance variables was partitioned into six principal components: (1) URBAN—proximity to nearest urban area or paved road; (2) FIRE—number of fires and area burned between 1980 and 1994 within 5 km of each study site; (3) CATTLE—located in a perennial cattle grazing allotment; (4) AGRI—proximity to nearest existing or abandoned agricultural area and sheep grazing allotments; (5) OHVS—intensity of OHV use; and (6) DIRTROAD—total length of dirt roads in the township section (Table 1). The proportion of variance in the raw data that each of these five variables accounted for was similar, ranging from 0.21 to 0.12.

Variance among productivity variables was partitioned into three principal components: (1) RAIN—average annual rainfall; (2) NATIVEBIOMASS—absolute biomass of native annual plants; and (3) NITR—total soil nitrogen (Table 1). The proportion of variance explained by each productivity variable ranged from 0.30 to 0.25.

Variance among native plant diversity variables was not partitioned into PCA variables because we only considered two unique raw predictor variables: (1) ANNDIV—annual plant diversity; and (2) PERDIV—perennial plant diversity. ANNDIV and PERDIV data were each normally distributed (Kolmogorov–Smirnov test,  $p \leq 0.05$ ) and non-heteroscedastic ( $F_{\max}$  test  $p > 0.20$ ).

The nine principal component variables (Table 1), plus the two diversity variables, were then used as predictor variables in multiple regression analyses. All disturbance, productivity, and diversity variables were analyzed simultaneously to determine which were the best predictors for each of the response variables. Elevation, latitude, and longitude were evaluated as covariates by adding them as variables in multiple regression analyses. The data were spatially autocorrelated, because within-site samples were more similar than between-site samples. Thus, average values from each study site were used in all analyses ( $n = 34$ ). Residuals of the predictor variables and covariates were normally distributed with constant variance ( $p < 0.05$ ) and were not transformed prior to analysis.

Final regression models were derived using a forward addition procedure sequentially adding predictor variables that produced the greatest increase in the  $F$ -ratio until the addition of more variables did not cause significant increases ( $p < 0.05$ ) (PROC REG in SAS, 1988). Similar sets of predictor variables were generated using backward elimination and stepwise procedures ( $p < 0.05$ ). However, we only reported results generated using the forward addition procedure. Significant patterns in the multiple regression analyses were evaluated further by plotting back-transformed response variables versus predictor variables or covariates. We used type III sums of squares to calculate  $F$ -ratios and used the type I error rate of  $p \leq 0.05$  as the criterion of statistical significance in all analyses.

### 3. Results

#### 3.1. Alien annual plant dominance

Alien species represented a small fraction of the total annual plant flora, but they comprised most of the total annual plant community biomass. When rainfall was high in



1995, only 6% (8 of 129) of the annual plant species were aliens (Appendix), but they comprised 66% of the 655 kg/ha total annual plant biomass. When rainfall was low in 1999, 27% (8 of 30) of the annual species were aliens (Appendix), but they comprised 91% of the 38 kg/ha annual plant biomass. *Bromus rubens*, *Schismus* spp., and *E. cicutarium* were the most abundant alien species during these two years, but their relative dominance varied between years. *Bromus rubens* dominated alien biomass during 1995 whereas *Schismus* spp. and *E. cicutarium* dominated during 1999 (Fig. 2). Four other alien species, the annual grasses *B. trinii* and *B. tectorum* and the mustards *Descurania sophia* and *Sisymbrium irio*, were sampled and included in total alien analyses. However, these species were not individually analyzed due to their low abundances, which collectively comprised <1% of the total alien biomass during both years. As for the 121 native annual species sampled during 1995, *Amsinckia tessellata* represented 5% of the total annual plant biomass and all other species each represented <3%. The 22 native species sampled during 1999 each comprised <1% of the total annual plant biomass.

The relative biomasses of the three dominant alien species also differed between microhabitats. The beneath-canopy microhabitat contained most of the biomass of *B. rubens* (52% in 1995, 94% in 1999), whereas the interspace microhabitat contained most of the biomass of *Schismus* spp. (92% in 1995 and 77% in 1999) and *E. cicutarium* (88% in 1995 and 65% in 1999).

Relative biomasses of the alien species also varied as the total biomass of alien annual plants increased. At low levels of alien annual plant biomass below approximately 400 kg/ha, *Schismus* spp. and *E. cicutarium* comprised most of the alien biomass. In contrast, at higher levels of alien biomass, *B. rubens* became increasingly more dominant during 1995 when total alien biomass ranged widely from 40 to 1430 kg/ha (Fig. 3). The relationships were not clear during 1999 when total alien biomass only ranged from 20 to 55 kg/ha. In general, *B. rubens* accounted for the majority of the alien annual plant biomass in 1995, whereas all three major alien species contributed about equally in 1999.

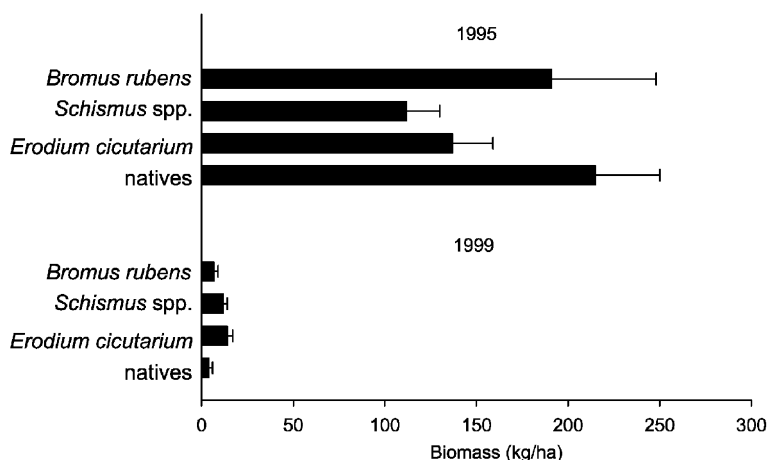


Fig. 2. Primary components of annual plant biomass, comprised of three alien species plus all natives combined (complete species list in the Appendix).

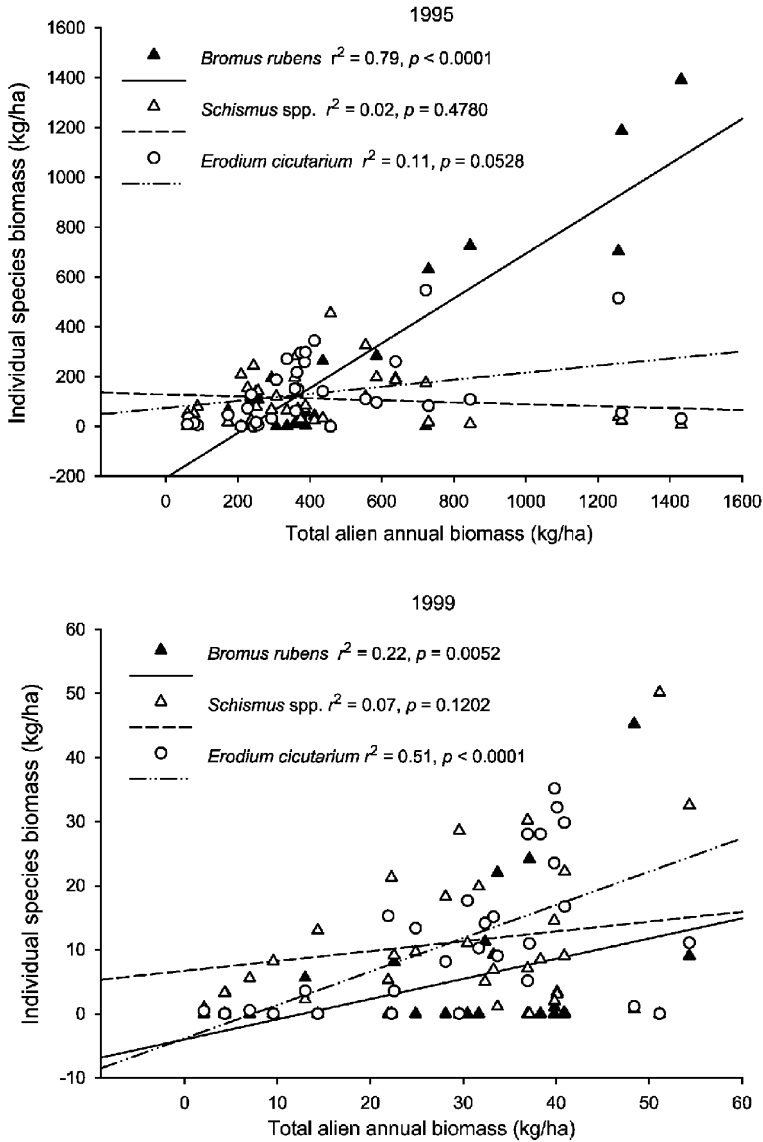


Fig. 3. Relationships between the three dominant alien plant species and total alien annual plant biomass.

### 3.2. Alien plant species richness patterns

Alien richness was positively correlated with DIRTROAD during 1995 and with NITR during 1999 (Table 2). NITR was also correlated with elevation (Table 3), but it remained as a significant predictor variable even after elevation was added as a covariate in the multiple regression analysis. Regression plots of the raw data also indicated that alien species richness increased significantly with dirt road dominance in 1995 and with soil

Table 2

Linear regression of alien plant species richness [ $\sqrt{(x+0.5)}$ ] as the response variable, and the predictor variables that remained using a forward selection procedure ( $p \leq 0.05$ )

|                | Standardized coefficients | Partial $R^2$ | d.f. | $F$   | $p$    |
|----------------|---------------------------|---------------|------|-------|--------|
| 1995           |                           |               |      |       |        |
| Alien richness | 0.49 DIRTROAD             | 0.24          | 1,32 | 10.21 | 0.0031 |
| 1999           |                           |               |      |       |        |
| Alien richness | 0.42 NITR                 | 0.17          | 1,32 | 6.90  | 0.0016 |

nitrogen in 1999 (Fig. 4). These results indicate that the number of alien species was highest where dirt road density was high during the year of high rainfall, and where soil nitrogen was high during the year of low rainfall. Thus, alien richness can be positively correlated with disturbance and productivity variables, but the importance of each can vary inter-annually.

### 3.3. Alien plant biomass patterns

Total alien biomass was positively correlated with FIRE and URBAN during 1995, but negatively correlated with ANNDIV and positively correlated with FIRE, NATIVEBIOMASS, and OHVHIST during 1999 (Table 4). Although some of these variables covaried with elevation (Table 3), their significance did not change when elevation was added to the regression analyses. These results indicate that disturbance and productivity can be positively correlated with alien biomass and that native plant diversity can be negatively correlated with alien biomass, but that the relative importance of each variable may differ between years.

FIRE was the only variable significantly correlated with alien biomass during both years (Table 4). It was not significantly correlated with any other predictor variables (Table 3). In addition, the patterns observed for total alien biomass were primarily due to significant correlations of alien annual grasses with FIRE during 1995 and 1999 (Table 4). Thus, frequency and size of fires were significantly correlated with biomass of alien plants, alien annual grasses in particular.

Biomass of *B. rubens* was positively correlated with PERDIV in 1995 and with PERDIV and FIRE in 1999 (Table 4). The positive relationship of *B. rubens* with PERDIV was likely due to the strong correlation of PERDIV with elevation (Table 3). When elevation was included as a covariate in the regression analyses, it was strongly correlated with *B. rubens* biomass in 1995 (partial  $R^2 = 0.44$ ,  $F_{1,32} = 25.35$ ,  $p < 0.0001$ ) and 1999 (partial  $R^2 = 0.46$ ,  $F_{1,32} = 26.10$ ,  $p < 0.0001$ ). PERDIV did not show up as a significant predictor variable in these covariate analyses, but FIRE remained significant during 1999 (partial  $R^2 = 0.09$ ,  $F_{1,32} = 5.16$ ,  $p = 0.0302$ ). Elevation was also positively correlated with a number of productivity and diversity variables (Table 3), which indicated that it represented a gradient comprised of many covarying factors. Thus, biomass of *B. rubens* was positively correlated with the elevational (productivity/diversity) gradient and frequency and size of fires.

Biomass of *Schismus* spp. was negatively correlated with PERDIV and NITR in 1995, and with PERDIV in 1999. However, PERDIV and NITR were also positively correlated

Table 3  
 Pearson product moment correlations of three covariates (latitude, longitude, and elevation) and 11 predictor variables, with significant correlations ( $n = 34$ ;  $p \leq 0.05$ ) in bold font

|            | Lat.        | Long.       | Elev.       | URBAN       | FIRE  | CATTLE      | AGRI | OHVS        | DIRTROAD | RAIN  | NATIVE BIOM | NITR | ANN DIV     | PER DIV |
|------------|-------------|-------------|-------------|-------------|-------|-------------|------|-------------|----------|-------|-------------|------|-------------|---------|
| Latitude   | 1.00        |             |             |             |       |             |      |             |          |       |             |      |             |         |
| Longitude  | <b>0.41</b> | 1.00        |             |             |       |             |      |             |          |       |             |      |             |         |
| Elevation  | 0.04        | 0.14        | 1.00        |             |       |             |      |             |          |       |             |      |             |         |
| URBAN      | 0.12        | 0.07        | <b>0.43</b> | 1.00        |       |             |      |             |          |       |             |      |             |         |
| FIRE       | -0.09       | -0.07       | 0.05        | 0.00        | 1.00  |             |      |             |          |       |             |      |             |         |
| CATTLE     | -0.31       | -0.42       | 0.32        | 0.00        | 0.00  | 1.00        |      |             |          |       |             |      |             |         |
| AGRI       | 0.27        | <b>0.35</b> | 0.04        | 0.00        | 0.00  | 0.00        | 1.00 |             |          |       |             |      |             |         |
| OHVS       | -0.06       | 0.32        | 0.02        | 0.00        | 0.00  | 0.00        | 0.00 | 1.00        |          |       |             |      |             |         |
| DIRTROAD   | 0.01        | 0.15        | 0.08        | 0.00        | 0.00  | 0.00        | 0.00 | 0.00        | 1.00     |       |             |      |             |         |
| RAIN       | <b>0.45</b> | <b>0.76</b> | -0.01       | 0.02        | -0.10 | <b>0.38</b> | 0.32 | <b>0.46</b> | 0.12     | 1.00  |             |      |             |         |
| NATIVEBIOM | 0.13        | 0.24        | <b>0.39</b> | 0.20        | -0.23 | 0.25        | 0.17 | -0.08       | 0.07     | 0.00  | 1.00        |      |             |         |
| NITR       | 0.01        | 0.06        | <b>0.46</b> | 0.02        | 0.33  | 0.16        | 0.03 | -0.01       | 0.21     | 0.00  | 0.00        | 1.00 |             |         |
| ANN DIV    | 0.06        | 0.17        | <b>0.49</b> | 0.31        | 0.01  | 0.04        | 0.26 | -0.17       | -0.18    | -0.10 | <b>0.45</b> | 0.37 | 1.00        |         |
| PER DIV    | -0.17       | -0.11       | <b>0.61</b> | <b>0.53</b> | 0.19  | 0.21        | 0.01 | -0.19       | 0.06     | -0.30 | 0.23        | 0.28 | <b>0.56</b> | 1.00    |

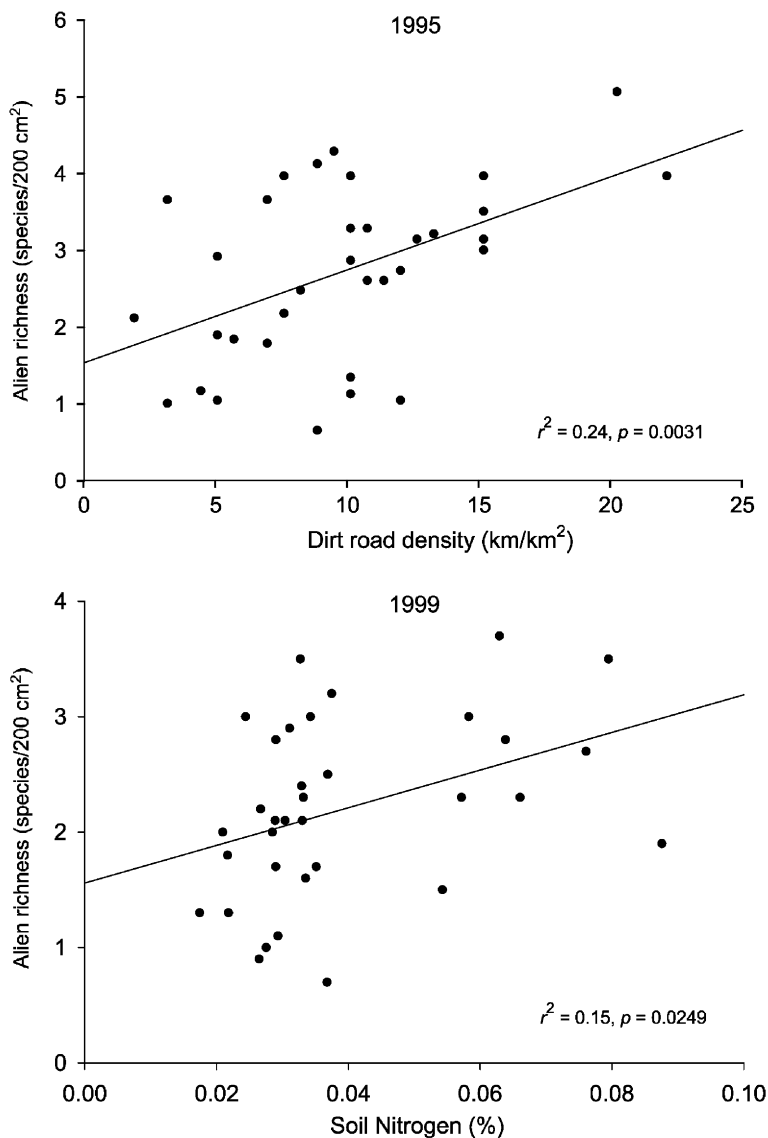


Fig. 4. Relationships of alien plant species richness with dirt road density and soil nitrogen.

with elevation (Table 3), and they dropped out as significant predictor variables when elevation was added as a covariate in the multiple regression analyses. Elevation was negatively correlated with the biomass of *Schismus* spp. in 1995 (partial  $R^2 = 0.35$ ,  $F_{1,32} = 17.45$ ,  $p < 0.0001$ ) and 1999 (partial  $R^2 = 0.43$ ,  $F_{1,32} = 24.26$ ,  $p < 0.0001$ ). Thus, elevation was the most robust predictor of the biomass of *Schismus* spp., with high levels at low elevations (Fig. 5).

Biomass of *E. cicutarium* was positively correlated with DIRTROAD in both 1995 and 1999 (Table 4). During both years the biomass of *E. cicutarium* increased as the density of

Table 4

Linear regression of alien biomass [ $\log(x+1)$ ] as the response variable and the predictor variables that remained using a forward selection procedure ( $p \leq 0.05$ ). Predictor variables are listed in the order they were entered into the equations, and those that were significant during both years for a given response variable are in bold font

| Response variables (biomass) | Standardized coefficients  | Partial $R^2$          | d.f. | $F$   | $p$    |
|------------------------------|--|------------------------|------|-------|--------|
| 1995                         |  |                        |      |       |        |
| Alien annuals                | <b>0.44 FIRE</b> + 0.32 URBAN                                    | 0.20, 0.10             | 2,31 | 6.54  | 0.0043 |
| Alien annual                 | 0.44 URBAN + <b>0.41 FIRE</b>                                    | 0.19, 0.17             | 2,31 | 8.66  | 0.0010 |
| grasses                      |  |                        |      |       |        |
| <i>Bromus rubens</i>         | <b>0.62 PERDIV</b>   | 0.39                   | 1,32 | 20.22 | 0.0001 |
| <i>Schismus</i> spp.         | − <b>0.45 PERDIV</b> − 0.33 NITR                                 | 0.29, 0.10             | 2,31 | 9.79  | 0.0005 |
| <i>Erodium cicutarium</i>    | <b>0.40 DIRTROAD</b>   | 0.16                   | 1,32 | 6.08  | 0.0192 |
| 1999                         |  |                        |      |       |        |
| Alien annuals                | −0.55 ANNDIV + <b>0.43 FIRE</b> + 0.43 NATIVEBIOM + 0.30 OHVHIST | 0.16, 0.11, 0.14, 0.08 | 4,29 | 6.93  | 0.0005 |
| Alien annual                 | 0.36 FIRE  | 0.13                   | 1,32 | 4.91  | 0.0339 |
| grasses                      |  |                        |      |       |        |
| <i>Bromus rubens</i>         | 0.58 PERDIV + <b>0.29 FIRE</b>                                   | 0.40, 0.08             | 2,31 | 14.52 | 0.0001 |
| <i>Schismus</i> spp.         | − <b>0.52 PERDIV</b>   | 0.28                   | 1,32 | 11.79 | 0.0017 |
| <i>Erodium cicutarium</i>    | <b>0.47 DIRTROAD</b>   | 0.22                   | 1,32 | 9.07  | 0.0050 |

dirt roads increased (Fig. 6). Hence, dirt road density was a reliable indicator of the biomass of *E. cicutarium*, especially considering that *E. cicutarium* and DIRTROAD were not significantly correlated with any other predictor or covariate variable (Table 3).

During both years *B. rubens* and *Schismus* spp. were negatively correlated with each other ( $r = 0.28$ ,  $p < 0.05$ ). This relationship was largely due to their contrasting relationships with elevation (Fig. 5). *Schismus* spp. had higher biomass below 800 m (1995) to 1000 m (1999), whereas *B. rubens* had higher biomass above these elevations during the respective years. *E. cicutarium* was not significantly correlated with *B. rubens*, *Schismus* spp., or elevation during 1995 or 1999. The negative correlations between *B. rubens* and *Schismus* spp. may have affected their individual correlations with the predictor variables. Therefore, individual regression analyses for each of the three alien species were evaluated with and without the other two species included as covariates. The regression results were similar whether or not other aliens were included in the analyses, indicating that covariance among alien species did not significantly obscure their individual correlations with the predictor and covariate variables.

## 4. Discussion

### 4.1. Dominance of alien annual plants

A relatively small proportion (~6%) of the annual plant species were aliens in this study, which is similar to the 9% alien species composition reported among all 1836 vascular plant species in the Mojave Desert at the end of the 1970s (Rowlands et al., 1982). If all species of vascular plants had been included in the present study, the proportional

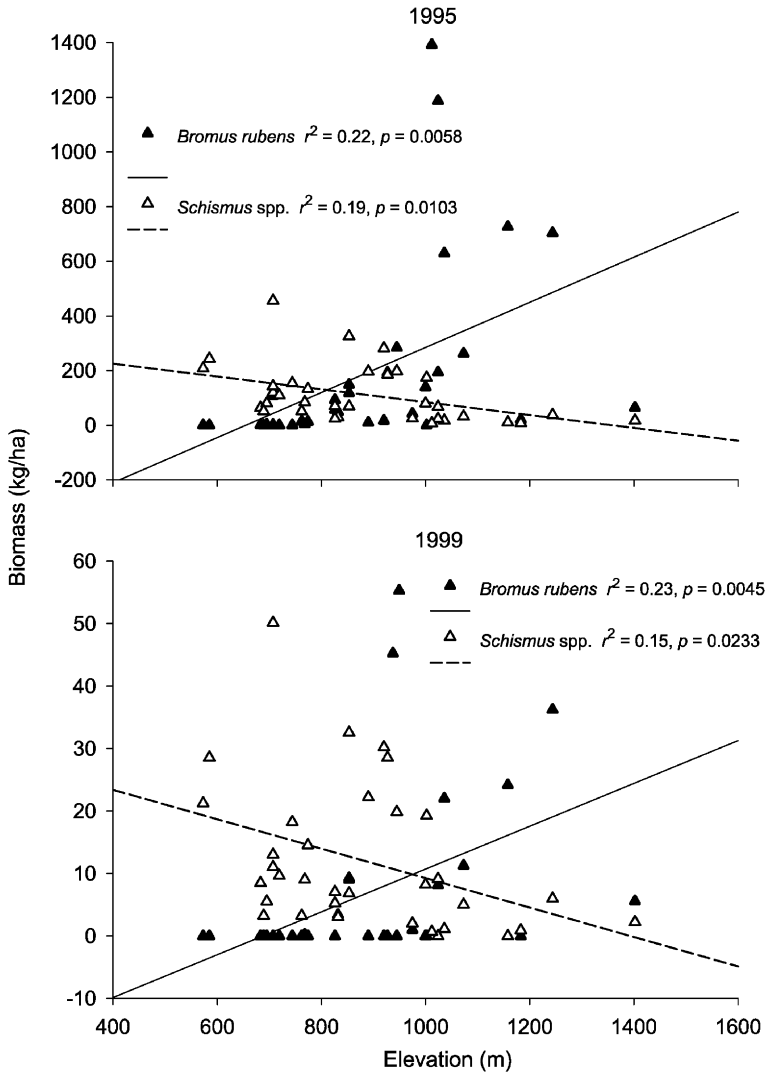


Fig. 5. Relationships of *Bromus rubens* and *Schismus* spp. biomass with elevation.

composition of aliens in the total flora would have been even lower than 6%, because relatively few alien perennial species occur in the Mojave Desert (Brooks and Esque, 2002) and none of them were encountered in our study. These results support other studies indicating that desert floras contain relatively few alien species compared to an average of 16% alien species composition across a wide range of other ecosystems, and a high of 32% in island ecosystems (Lonsdale, 1997, 1999).

Although aliens contribute relatively few species to the annual plant flora, they comprise the vast majority of the total annual plant community biomass in the Mojave Desert, especially during years of low rainfall. It has been suggested that there are proportionally more aliens in the annual plant community during years of low rainfall due to the less

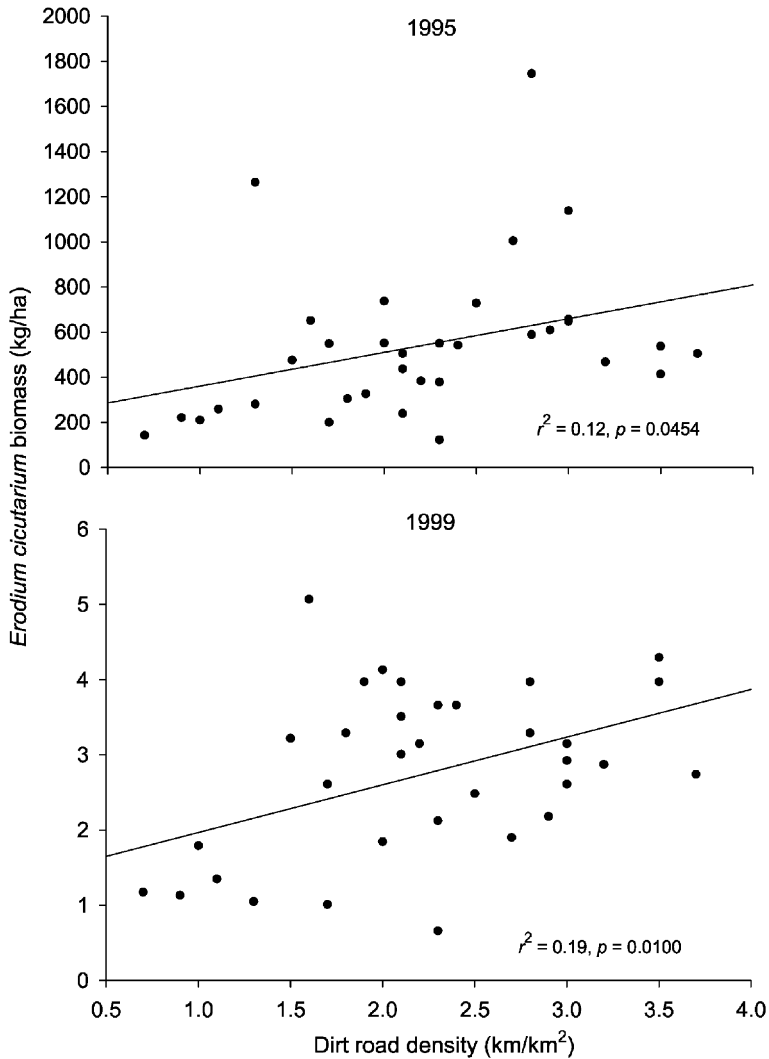


Fig. 6. Relationship between biomass of *Erodium cicutarium* and density of dirt roads.

stringent germination requirements of alien compared to native species (Brooks, 1999b). In the study by Brooks (1999b), proportional alien biomass was 96% during a year when rainfall was low (52% of the long-term average) and 34% when rainfall was high (207% of the long-term average) at a site in the western Mojave Desert. Those values are similar to what was reported in our study from multiple sites across the central, southern, and western Mojave Desert: 91% alien biomass when rainfall was low (48% of the long-term average) and 66% alien biomass when rainfall was high (200% of the long-term average). However, another study from the west-central Mojave Desert indicates that proportional alien cover can also be similar during 2 years of contrasting rainfall, reporting 56% (interspace) and 76% (beneath-canopy) proportional alien cover when rainfall was relatively high (165% of the long-term average), and 68% (interspace) and



72% (beneath-canopy) proportional alien cover when rainfall was relatively low (43% of the long-term average) (Brooks et al., 2006). Thus, the interannual variation in proportional dominance of alien species may be affected by factors other than just rainfall during the current year.

Low rainfall amounts during previous years may also affect the proportional biomass of aliens. Low rainfall may deplete the alien plant seedbank when seeds germinate but plants do not survive to reproduce (Brooks and Minnich, 2006). This is especially prevalent in alien species that did not evolve in arid environments (e.g. *B. rubens*; Brooks and Minnich, 2006). A few years of low rainfall may also allow levels of limiting soil nutrients such as nitrogen to build up in the soil, providing enhanced amounts of nutrients for plants during the first year of high rainfall following drought (F. Vasek, pers. comm.). If the alien seedbank survives a drought, then the aliens may be around to benefit from enhanced nitrogen levels following drought (Brooks, 2003). However, if the alien seedbank are depleted during a drought, then natives would likely experience higher productivity following drought. Ultimately, seedbank dynamics, soil nutrient availability, and rainfall patterns probably combine with other factors, such as time since invasion, disturbance history, and interspecific competitive relationships, to determine the relative dominance of alien annual plants at a particular site.

Most studies indicate that *Schismus* spp. and *E. cicutarium* are more abundant than *B. rubens* in the central, southern, and western Mojave Desert, which contrasts with the results of our study. For example, *S. barbatus* and *E. cicutarium* were the only alien species reported by Davidson and Fox (1976), and these species comprised 30–83% of total annual plant density during 1973 at two sites in the western Mojave Desert. These two species were also the only aliens reported by Webb and Stielstra (1979), and comprised 7–30% of total annual plant density during 1978 averaged over two other sites in the western Mojave Desert. *Schismus barbatus* and *E. cicutarium* comprised 48–99% of all annual plant biomass sampled and *B. rubens* was only sporadically encountered during 1981–1985 at a site in the central Mojave Desert (Samson, 1986). *Schismus barbatus* and *E. cicutarium* comprised 25–77%, whereas *B. rubens* comprised <1%, of total annual plant biomass during 1991–1995 at a site in the western Mojave Desert (Jennings, 1993; Brooks, 1995, 1999b). *Schismus* spp. and *E. cicutarium* comprised 90% and 2% of total annual plant biomass during 1998 at a site in the central Mojave Desert (Ofstedal et al., 2002). At a site in the west-central Mojave Desert, *Schismus* spp., *E. cicutarium*, and *B. rubens* comprised 27%, 33%, and 8% of the total annual plant biomass during 1998 respectively; and they constituted 36%, 35%, and 6% of total annual plant biomass during 2000 respectively (Brooks et al., 2006). These previous studies consistently reported *Schismus* spp. and *E. cicutarium* as the dominant alien species during various years of contrasting rainfall between 1973 and 2000. However, they were mostly conducted at relatively low elevations (<800–1000 m) where, according to the results our study (Fig. 5), *B. rubens* is expected to be least abundant.

One exception to this elevational pattern of alien species dominance was reported from low elevation sites (approximately 150 m) at the north-western edge of the Colorado Desert close to the more mesic regions of the San Jacinto Mountains. Cover estimates in recently burned and unburned creosotebush scrub were 32% and 40%, respectively, for *B. rubens*, and 25% and 17%, respectively, for *S. barbatus* (Brown and Minnich, 1986). These results suggest that *B. rubens* may be more abundant than *Schismus* spp. at regional ecotones with more mesic regions, in addition to being more abundant at higher elevations,

which are both consistent with general observations throughout the region (Brooks and Minnich, 2006; M. Brooks, pers. obs.).

#### 4.2. Correlations of alien plants with disturbance, productivity, and native plant diversity

Disturbance variables were more reliable than productivity or plant community diversity variables in predicting species richness and biomass of alien annual plants across multiple sites in our study. This conclusion differs from a previous study in which productivity gradients associated with shrubs and interspaces between shrubs, and topographic features, were better predictors of alien species richness and biomass than were the combined effects of multiple disturbance factors within a single site in the western Mojave Desert (Brooks, 1999b). In our study, the proportional biomass of aliens also varied significantly between the high productivity area beneath shrubs (beneath-canopy) and the low productivity area between shrubs (interspace). However, our analyses were not specifically designed to evaluate local differences within sites, and focused instead on regional differences among sites. We conclude that disturbance levels may be a better indicator of alien dominance at regional scales among sites, whereas productivity levels may be a better indicator of dominance at local scales within sites. Exceptions to this rule within sites is where local disturbance gradients are extreme, such as along roadsides, near livestock watering sites, camp-sites, mines, and OHV open riding areas, and at the margins of urbanized and agricultural areas.

The positive correlations of dirt road density with alien species richness and biomass of *E. cicutarium* were one of the strongest relationships we found. In another study from the Mojave Desert, *E. cicutarium* comprised 55–75% of annual plant biomass near roads, with *Schismus* spp. and *B. rubens* next in dominance (Johnson et al., 1975). *Erodium cicutarium* was also one of the three most abundant alien forbs along paved road verges on the semi-arid Colorado Plateau (Gelbard and Belnap, 2003).

It is widely known that roadsides are one of the primary pathways for plant invasions into desert regions (Amor and Stevens, 1976; Brooks and Pyke, 2001). Roads facilitate dispersal of alien plant seeds (Trombulak and Frissell, 2000). Four-wheel drive vehicles carry significantly more seeds than 2-wheel drive vehicles (Lonsdale and Lane, 1994). Off-highway vehicle use tends to be concentrated around dirt roads and other pathways of travel away from roadsides, such as washes and utility rights-of-way (Matchett et al., 2004). This may explain why there are more alien species near dirt roads. In addition, dirt roads are often associated with elevated levels of livestock grazing and other human-related activities (FWS, 1994). Roadsides not only experience high levels of disturbance, but they also have high levels of productivity from rainfall flow off of road surfaces and onto adjacent roadside verges (Johnson et al., 1975; Starr, 2002). Where road densities are high, alien richness and biomass may increase from the combined effects of high alien biomass near roads, increased dispersal of seeds along and away from roads by vehicles, decreased distances from roads to other areas of the landscape, and locally high productivity levels along roadsides.

Our study provides a positive link of fire frequency and fire size with alien annual grasses in the Mojave Desert. This positive relationship is due to the greater flammability of grasses compared to most other types of plants. Annual grasses are generally more flammable than forbs (Kaufmann and Uhl, 1990), and alien annual grasses in the Mojave Desert promote the spread of fire by increasing the continuity and persistence of fine fuels

in the interspaces between perennial plants (Brooks, 1999a). *Bromus rubens* provides the bulk of these fine fuels, especially at higher elevations, although *Schismus* spp. can promote fires as well, particularly at lower elevations where *B. rubens* is less abundant. (Brooks, 1999a, 2000b, c; Brooks and Minnich, 2006). Most large fires in the Mojave Desert occur in remote wildland areas (Brooks and Esque, 2002). These fires tend to occur at higher elevations where fuel loads from *B. rubens* reach their peak (e.g. above 800 m in our study, Fig. 5). Prior to the invasion of annual grasses, arid deserts of North America were relatively fire-resistant due to wide spacing between perennial shrubs and bunchgrasses, and low annual plant biomass between them (Humphrey, 1974; O'Leary and Minnich, 1981; Brooks and Minnich, 2006). Fires have become much more frequent in a few regional hot-spots within the Mojave Desert, with serious negative implications for native plants and animals (Brooks and Pyke, 2001; Brooks and Esque, 2002).

The relationships of alien plants with variables of productivity and native plant diversity were difficult to evaluate due to multiple covarying factors. Soil nitrogen was positively correlated with alien richness and native biomass was positively correlated with total alien biomass, but negatively correlated with the biomass of *Schismus* spp. Perennial plant diversity was positively correlated with *B. rubens*, but negatively correlated with *Schismus* spp. Perhaps a more informative predictor variable was elevation, which was positively correlated with the diversity and productivity variables, species richness, and biomass of *B. rubens*, but negatively correlated with biomass of *Schismus* spp. Rainfall increases with elevation in the Mojave Desert (Rowlands, 1978, 1995), and species diversity is positively correlated with productivity at low to moderately productive sites (Rosenzweig and Abramsky, 1993; Huston, 1994). Therefore, this elevation gradient can also be considered a productivity gradient. Although the data from *B. rubens* support the hypothesis that aliens are positively correlated with productivity levels, data from *Schismus* spp. indicates that aliens can also be negatively correlated with productivity at large regional scales. Similar results were reported at a small local scale within a site in the western Mojave Desert (Brooks, 1999b). It appears that the inherent productivity of a region or site can influence the dominance and possibly the invasion potential of alien species.

Native plant diversity was not a good independent indicator of alien plant dominance in the Mojave Desert. Perennial plant diversity correlated with some alien variables, but it also covaried strongly with elevation as discussed in the previous paragraph. Annual plant diversity was significantly correlated with total biomass of alien annuals during 1999, but it too was strongly correlated with elevation.

Environmental correlates varied somewhat between years in our study. This variation demonstrates the importance of evaluating patterns of annual plant invasions over multiple years (Venable et al., 1993; Tielbörger and Kadmon, 1997). Short-term correlative patterns are more likely to be consistent among years if there are always alien seedlings to sample, the relative dominance of aliens among sites remains relatively constant, and gradients in predictor variables remain unchanged. These conditions appear to be possible, based on 6 years of unchanged among-site dominance patterns of annual plants reported from the northern Mojave Desert (Bowers, 1987). Long-term correlative patterns may change as gradients in the relative dominance of aliens and predictor variables change following the spread of aliens into new areas, the arrival of new species with different environmental affinities, and changes in the characteristics of environmental variables. Therefore, the patterns described in our study can be considered consistent for the short-term, but may have been different in the past, and may change in the future.

### 4.3. Management implications

The results of our study and other studies (Samson, 1986; Jennings, 1993; Brooks, 1995, 1999b; Oftedal et al., 2002; Brooks et al., 2006) suggest that the proportional biomass of alien species in the annual plant community may seldom drop below 50% during years of above-average rainfall, and is typically much higher during years of low rainfall. These studies were conducted in relatively undisturbed areas of the Mojave Desert, so their results can be used to estimate the baseline dominance of alien annual plants across the region. This baseline is useful in defining management targets related to alien annual plants, which we recommend being set at 50% proportional alien biomass. This target can be used to define project goals for alien plant control or native plant restoration projects in particular, and land management planning documents in general.

Minimizing the density of dirt roads may minimize dominance of alien annuals, alien species richness, and the biomass of *E. cicutarium* in particular. Reduced biomass of alien annual grasses, *B. rubens* in particular, may reduce the frequency and size of fires (Brooks and Pyke, 2001; Brooks and Esque, 2002; Brooks and Minnich, 2006). Protection of lands from continuing and new disturbances can also have beneficial effects by reducing dominance of alien annual plants (Brooks, 1995, 1999b, 2000d).

The prevention of new invasions should be a priority for land managers, because control is most feasible at the early stages of invasion. Monitoring to detect changes in the status of alien species should focus on regions of high road density or fire frequency, especially near urban or OHV areas. Within monitoring sites, efforts to detect new species should focus on areas of high productivity such as washes, roadsides, and beneath-canopy microhabitats. Alien plants that originated in mesic ecosystems are more likely to invade areas where rainfall is high, such as at high elevations or at regional ecotones between the Mojave Desert and other more mesic ecoregions. However, alien plants that evolved in arid ecosystems can potentially invade a wider range of sites (e.g., Jackson, 1985). Once new invaders are detected, decision support tools can help land managers evaluate them for their potential ecological impacts and prioritize them for control (Warner et al., 2003; Morse et al., 2004).

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## Appendix. Annual plant species sampled during April and May, 1995 and 1999

Table A1.

Table A1

| Species   | 1995 | 1999 | Species                         | 1995 | 1999 |
|---|------|------|---------------------------------|------|------|
| <i>Amsinckia tessellata</i>                                 | x    | x    | <i>Garea canescens</i>          | x    |      |
| <i>Antirrhinum filipes</i>                                  | x    |      | <i>Gilia brecciarum</i>         | x    |      |
| <i>Aristida adscensionis</i>                                | x    | x    | <i>Gilia latiflora</i>          | x    |      |
| <i>Astragalus acutirostris</i>                              | x    |      | <i>Gilia malior</i>             | x    |      |
| <i>Astragalus didymocarpus</i>                              | x    |      | <i>Gilia minor</i>              | x    | x    |
| <i>Astragalus lentiginosus</i>                              | x    |      | <i>Glyptopleura marginata</i>   | x    |      |
| <i>Bromus madritensis</i> subsp. <i>rubens</i> <sup>a</sup> | x    | x    | <i>Langloisia setosissima</i>   | x    |      |
| <i>Bromus tectorum</i> <sup>a</sup>                         | x    | x    | <i>Lasthenia californica</i>    | x    | x    |
| <i>Bromus trinitii</i> <sup>a</sup>                         | x    | x    | <i>Lepidium flavum</i>          | x    |      |
| <i>Camissonia boothii</i>                                   | x    |      | <i>Lepidium lasiocarpum</i>     | x    |      |
| <i>Camissonia campestris</i>                                | x    |      | <i>Linanthus bigelovii</i>      | x    |      |
| <i>Camissonia claviformis</i>                               | x    |      | <i>Linanthus dichotomus</i>     | x    |      |
| <i>Camissonia palmeri</i>                                   | x    |      | <i>Loeseliastrum matthewsii</i> | x    |      |
| <i>Caulanthus cooperi</i>                                   | x    |      | <i>Loeseliastrum schottii</i>   | x    |      |
| <i>Caulanthus inflatus</i>                                  | x    |      | <i>Lotus humistratus</i>        | x    | x    |
| <i>Centrostegia thurberi</i>                                | x    |      | <i>Lotus strigosus</i>          | x    |      |
| <i>Chaenactis carphoclinia</i>                              | x    |      | <i>Lupinus concinnus</i>        | x    |      |
| <i>Chaenactis fremontii</i>                                 | x    | x    | <i>Lupinus microcarpus</i>      | x    |      |
| <i>Chaenactis macrantha</i>                                 | x    |      | <i>Lupinus sparsiflorus</i>     | x    |      |
| <i>Chaenactis stevioides</i>                                | x    | x    | <i>Malacothrix coulteri</i>     | x    |      |
| <i>Chamaesyce albomarginata</i>                             | x    |      | <i>Malacothrix glabrata</i>     | x    |      |
| <i>Chamaesyce polycarpa</i>                                 | x    |      | <i>Malvestrum exile</i>         | x    |      |
| <i>Chorizanthe brevicornu</i>                               | x    |      | <i>Mentzelia affinis</i>        | x    |      |
| <i>Chorizanthe rigida</i>                                   | x    |      | <i>Mentzelia albicaulis</i>     | x    |      |
| <i>Chorizanthe watsonii</i>                                 | x    |      | <i>Mentzelia eremophila</i>     | x    |      |
| <i>Coreopsis calliopsidea</i>                               | x    |      | <i>Mentzelia veatchiana</i>     | x    |      |
| <i>Cryptantha angustifolia</i>                              | x    |      | <i>Mimulus bigelovii</i>        | x    |      |
| <i>Cryptantha barbiger</i>                                  | x    |      | <i>Mirabilis bigelovii</i>      | x    |      |
| <i>Cryptantha circumscissa</i>                              | x    | x    | <i>Monoptilon bellidifforme</i> | x    |      |
| <i>Cryptantha dumetorum</i>                                 | x    |      | <i>Monoptilon bellioides</i>    | x    |      |
| <i>Cryptantha maritime</i>                                  | x    |      | <i>Nama demissum</i>            | x    |      |
| <i>Cryptantha micrantha</i>                                 | x    |      | <i>Nemacladus glanduliferus</i> | x    |      |
| <i>Cryptantha nevadensis</i>                                | x    | x    | <i>Nemacladus rubescens</i>     | x    |      |
| <i>Cryptantha pterocarya</i>                                | x    |      | <i>Nemacladus sigmoideus</i>    | x    |      |
| <i>Cuscuta</i> spp.   | x    |      | <i>Oxytheca perfoliata</i>      | x    |      |
| <i>Descurainia pinnata</i>                                  | x    | x    | <i>Parishella californica</i>   | x    |      |
| <i>Descurainia sophia</i> <sup>a</sup>                      | x    | x    | <i>Pectocarya penicillata</i>   | x    |      |
| <i>Dichelostemma capitatum</i>                              | x    |      | <i>Pectocarya platycarpa</i>    | x    | x    |
| <i>Eremalche rotundifolium</i>                              | x    |      | <i>Pectocarya recurvata</i>     | x    |      |
| <i>Eriastrum eremicum</i>                                   | x    |      | <i>Pectocarya setosa</i>        | x    | x    |
| <i>Eriastrum</i> spp.                                       | x    |      | <i>Phacelia crenulata</i>       | x    |      |
| <i>Eriogonum angulosum</i>                                  | x    |      | <i>Phacelia distans</i>         | x    |      |
| <i>Eriogonum deflexum</i>                                   | x    |      | <i>Phacelia fremontii</i>       | x    | x    |
| <i>Eriogonum gracillimum</i>                                | x    |      | <i>Phacelia ivesiana</i>        | x    |      |
| <i>Eriogonum inflatum</i>                                   | x    |      | <i>Phacelia tanacetifolia</i>   | x    | x    |
| <i>Eriogonum maculatum</i>                                  | x    |      | <i>Pholistoma membranaceum</i>  | x    |      |
| <i>Eriogonum nidularium</i>                                 | x    |      | <i>Plagiobothrys canescens</i>  | x    |      |

Table A1 (continued)

| Species                                | 1995 | 1999 | Species                               | 1995 | 1999 |
|--|------|------|---------------------------------------|------|------|
| <i>Eriogonum pusillum</i>              | x    |      | <i>Plagiobothrys jonesii</i>          | x    |      |
| <i>Eriogonum reniforme</i>             | x    |      | <i>Plantago ovata</i>                 | x    |      |
| <i>Eriogonum thomasi</i>               | x    |      | <i>Prenanthes exiguua</i>             | x    |      |
| <i>Eriogonum trichopes</i>             | x    |      | <i>Rafinesquia neomexicana</i>        | x    |      |
| <i>Eriophyllum ambiguum</i>            | x    |      | <i>Salvia columbariae</i>             | x    |      |
| <i>Eriophyllum pringlei</i>            | x    |      | <i>Schismus arabicus</i> <sup>a</sup> | x    | x    |
| <i>Eriophyllum wallacei</i>            | x    | x    | <i>Schismus barbatus</i> <sup>a</sup> | x    | x    |
| <i>Erodium cicutarium</i> <sup>a</sup> | x    | x    | <i>Sisymbrium irio</i> <sup>a</sup>   | x    | x    |
| <i>Erodium texanum</i>                 | x    |      | <i>Stephanomeria parryi</i>           | x    |      |
| <i>Eschscholzia glyptosperma</i>       | x    |      | <i>Streptanthella longirostris</i>    | x    | x    |
| <i>Eschscholzia minutiflora</i>        | x    | x    | <i>Stylocline</i> spp.                | x    |      |
| <i>Eucrypta micrantha</i>              | x    |      | <i>Syntrichopappus fremontii</i>      | x    |      |
| <i>Filago depressa</i>                 | x    | x    | <i>Tiquilia nuttallii</i>             | x    |      |
| <i>Filago</i> spp.                     | x    | x    | <i>Tiquilia plicata</i>               | x    |      |
| <i>Gilia ochroleuca</i>                | x    |      | <i>Tropidocarpum gracile</i>          | x    | x    |
| <i>Gilia sinuate</i>                   | x    |      | <i>Vulpia microstachys</i>            | x    | x    |
| <i>Gilia</i> spp.                      | x    |      | <i>Vulpia octoflora</i>               | x    | x    |
| <i>Gilia stellata</i>                  | x    |      |                                       |      |      |

<sup>a</sup>Alien species.

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