

The association of native and non-native annual plants with *Larrea tridentata* (creosote bush) in the Mojave and Sonoran Deserts

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ABSTRACT

Creosote bushes (*Larrea tridentata*) form islands of fertility that influence annual plant abundances in desert ecosystems, and the distribution of native and non-native annuals with respect to creosote may differ. We established plots on the north and south facing sides of *L. tridentata* in the Mojave and Sonoran Deserts within four different microhabitats spanning from under the shrub canopy into the open. We counted native and non-native annuals twice during the winter growing season to determine the effects of *L. tridentata* on the spatial distribution of native and non-native annuals. In both deserts, annual plant abundances were higher on the north side of *L. tridentata* and in open areas. Native annuals in the Mojave were most abundant near the edge of the shrub canopy, whereas native annuals in the Sonoran were most abundant in open areas. The effects of *L. tridentata* fertility islands on annual abundances were not consistent between the two deserts we studied. Our study emphasizes the importance of research on native and non-native annuals in multiple regions before generalizations can be made about the effects of *L. tridentata* on annual plant abundances in desert scrub ecosystems.

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1. Introduction

The concept of shrubs as fertility islands in arid and semi-arid ecosystems is well established (e.g. Schlesinger et al., 1996), and heterogeneity in soil resources associated with fertility islands may affect the distribution of annual plants (Brooks, 1999a; Esque et al., 2010). Soil organic matter, soil nitrogen, nitrogen mineralization and soil phosphorus are often higher under the shrub canopy than in open spaces among shrubs (e.g. Charley and West, 1975; Ewing et al., 2007; Schlesinger et al., 1996; Thompson et al., 2005). Solar radiation and soil temperature may be lower under shrubs than in the open (Forseth et al., 2001), but shrubs have variable effects on soil moisture, which may be higher (Thompson et al., 2005), lower (e.g. Forseth et al., 2001) or similar (e.g. Callaway et al., 1996; Ewing et al., 2007) under shrubs compared to open spaces. In addition, differences in soil characteristics under shrub canopies and in the open can depend on the side of the shrub that is sampled (Brooks, 1999a; Walker et al., 2001).

Spatial heterogeneity in resource availability associated with fertility (i.e. shrub) islands contributes to positive (i.e. facilitative) and/or negative (i.e. competitive) effects of shrubs on annual plants (e.g. Aguiar and Sala, 1994; Holzapfel and Mahall, 1999). Biomass of annual plants in arid ecosystems is often higher under shrub canopies than in the open (e.g. Halvorson and Patten, 1975; Muller, 1953; Patten, 1978; Shmida and Whittaker, 1981; Went, 1942), but shrub removal can cause an increase in annual plant densities (Facelli and Temby, 2002). Facilitative and competitive effects of shrubs occur simultaneously (e.g. Callaway, 1994; Facelli and Temby, 2002; Holmgren et al., 1997; Holzapfel and Mahall, 1999), and the importance of one effect over the other depends on the intensity of abiotic stress (Bertness and Callaway, 1994). For example, the positive effects of shrubs became more important along an environmental gradient from mesic to arid sites (Holzapfel et al., 2006). In a single site, however, increasing annual rainfall shifted the effects of shrubs in a positive direction (Tielbörger and Kadmon, 2000), suggesting that broad landscape patterns may not be applicable to local environments.

The dynamics of the facilitation–competition relationship between shrubs and annual plants may also depend on the identity of the annual species in question (Callaway, 1994). Non-native annual grasses and forbs have invaded the arid regions of western North America (Brooks, 1999a; D'Antonio and Vitousek, 1992; Schutzenhofer and Valone, 2006), and they can have high

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biomass under shrubs (Holzapfel and Mahall, 1999). Contrary to native annuals, however, non-native annuals often have higher biomass in the open areas between shrubs than under the shrub canopy (Brooks, 1999a, 2000). Understanding the effects of shrubs on non-native plant abundances is important considering that the spread of non-natives contributes to the establishment of continuous vegetation cover, which can facilitate fire spread in desert shrublands (e.g. Brooks, 1999b; Brooks, 2002).

Creosote bush, *Larrea tridentata* (DC.) Cov. (hereafter *Larrea*), is the dominant shrub throughout the arid regions of western North America. Numerous studies have documented that *Larrea* forms islands of fertility (e.g. Bolling and Walker, 2002; Brooks, 1999a; Ewing et al., 2007; Schlesinger et al., 1996). Much of the research on creosote bush fertility islands and native and non-native annuals has been conducted in the Chihuahuan and Mojave Deserts (e.g. Brooks, 2000; Schlesinger et al., 1996), but little is known about fertility islands and annuals in the Sonoran Desert (but see Halvorson and Patten, 1975; Patten, 1978).

Our objective was to determine how *Larrea* affects the abundance of native and non-native winter annuals in both the Mojave and Sonoran Deserts. We hypothesized that: (1) annuals are more abundant under the north, rather than the south, side of *Larrea* due to the positive effects of greater shading (Schenk and Mahall, 2002) and higher nitrogen availability (Brooks, 1999a); (2) the abundance of native annuals is higher under the *Larrea* canopy than in the open because of the facilitative effects of shrubs in arid ecosystems (e.g. Holzapfel et al., 2006); and (3) the abundance of non-native annuals is higher in the open than under the *Larrea* canopy because non-native species are able to exploit microhabitats not dominated by native species and root-mediated *Larrea* allelopathy (Mahall and Callaway, 1992) may have a greater effect on non-native species. Although the life stage of interacting species may affect whether interactions are facilitative or competitive (e.g. Morris and Wood, 1989), we expected *Larrea* to have the same effects on annual plant abundances in the beginning and end of the growing season (i.e. at the seedling and reproductive stages) due to the small stature of annual plants relative to *Larrea* regardless of life stage. In addition, we expected the distribution of annuals in relation to *Larrea* to be similar in the Mojave and Sonoran Deserts because: (1) the positive effects of shrubs vary with aridity (Holzapfel et al., 2006), and mean annual precipitation is similar in the Mojave and Sonoran Deserts; and (2) non-native annuals can create patches of biomass that connect shrubs and facilitate fire spread in desert shrublands (e.g. Brooks, 1999b; Brooks, 2002), and there is similar concern about the effects of non-native annuals on fire frequency and spread in both the Mojave and Sonoran Deserts (Brooks, 1999a; Schutzenhofer and Valone, 2006; R. Whittle, personal communication).

2. Materials and methods

2.1. Study sites

Our study site in the Mojave Desert (35°9'21" N, 116°53'6" W, 865 m MSL) is located within the Fort Irwin National Training Center, north of Barstow, California. Mean annual temperature is 17.7 °C and mean annual precipitation is 147 mm (Data for Goldstone Echo 2, 22 km N of our study site, Western Regional Climate Center, www.wrcc.dri.edu). Most precipitation falls during the winter and spring. The study site is an east-facing bajada dominated by *L. tridentata* (DC.) Cov. and *Ambrosia dumosa* (A. Gray) Payne. Soils are young and intermediate aged alluvial grus (decomposed granite; Amoroso and Miller, 2006).

Our study site in the Sonoran Desert (32°41'49" N, 112°50'22" W, 322 m MSL) is located within the Barry M. Goldwater Range,

south of Gila Bend, Arizona. Mean annual temperature is 22.7 °C and mean annual precipitation is 153.9 mm (Data for Gila Bend, 29 km NNE of our study site, Western Regional Climate Center, www.wrcc.dri.edu). This site often has two wet seasons, with rainfall during both the summer and winter. *Larrea* is the dominant species; other shrub species are scarce. Soils are coarse-loamy, hyperthermic, typic hypsicalcids (U.S. Department of Agriculture, 2005).

2.2. Experimental design

In September 2010, we established an 83 m × 130 m study site in both the Mojave and Sonoran Deserts. Within each site, we selected 168 focal *Larrea* individuals, excluding the smallest and largest individuals, and established transects beginning under each shrub and extending either north or south into the open area among shrubs; we installed two transects in the same direction at each shrub (Fig. 1a). In the Mojave site, some *A. dumosa* individuals were close to focal *Larrea* shrubs, but transects were established to avoid the influence of *A. dumosa* as much as possible. Plots (20 × 20 cm; 1344 in each desert) were established along each transect in four microhabitats: under the canopy (UC), at the canopy drip line (CD), in the open inter-shrub area near the focal shrub (ON) and in the open inter-shrub area far from the focal shrub (OF; Fig. 1a). These microhabitats were chosen to span from high shrub influence under the canopy to low shrub influence in the open far from the shrub. The location of the canopy drip line in the transect direction was estimated visually, and because the CD plot was centered on the canopy drip line (Fig. 1b), the distance from the UC plot to the CD plot was dictated by the canopy length in the transect direction (i.e. north or south); focal shrubs had a minimum canopy length of 35 cm in the transect direction to accommodate the UC and CD plots. Variation in canopy size among shrubs led to variation in the distance between the UC and CD plots, but the distance between other plots was consistent among shrubs, and all transects extend 150 cm from the canopy drip line into the inter-shrub area (Fig. 1b). Within site and between site differences in canopy size – focal *Larrea* individuals were larger, on average, in the Mojave site (mean + se; length = 229.8 + 6.6 cm, width = 183.7 + 4.5 cm) than in the Sonoran site (mean + se; length = 162.4 + 3.2 cm, width = 137.1 + 2.7 cm; E. Mudrak, unpublished data) – caused total transect length to range from 184 to 308 cm (mean = 221 cm) in the Mojave site and from 180 to 266 cm (mean = 206 cm) in the Sonoran site.

We installed weather stations (WeatherHawk 232, WeatherHawk, Logan, Utah) at both field sites. The weather station in the Mojave site began collecting data on 29 September, 2010, and the weather station in the Sonoran site began collecting data on 20 November, 2010. Measurements of rainfall and temperature were recorded at 15-min intervals in the Mojave site and at 1-hr intervals in the Sonoran site. Rainfall measurements were used to determine when to conduct seedling censuses.

2.3. Plant censuses

In both deserts, we counted annual plants in each plot ($n = 1344$ per desert) two times during the 2010–11 winter growing season. The first census was conducted after the first large winter rainfall event to assess seedling recruitment; previous research in the Mojave Desert has found that 15–25 mm of rainfall triggers scattered germination (Beatley, 1974). The second census was scheduled to coincide with flowering of annuals. Hereafter, these will be referred to as the seedling and reproductive censuses, even though not all individuals were at adult stage or in flower during the second census. In the Mojave site, the seedling census was

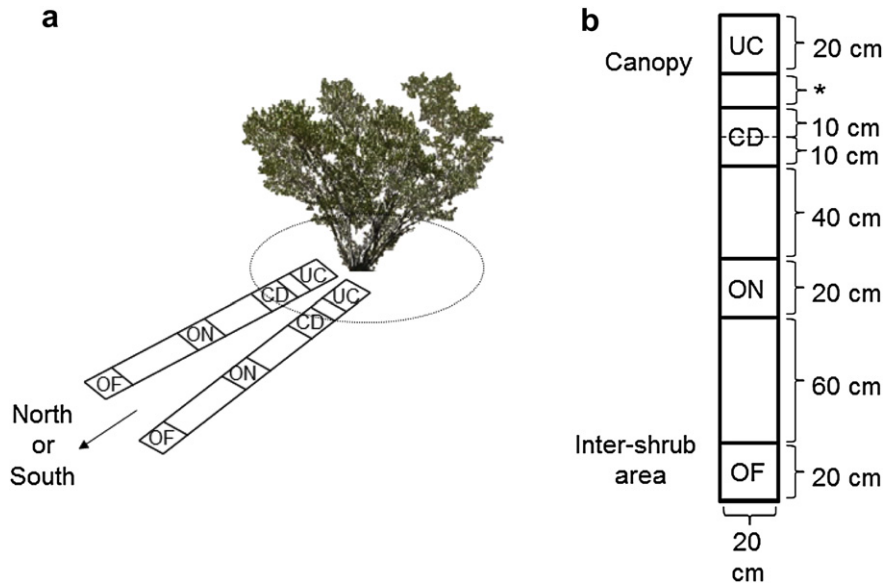


Fig. 1. Shrub diagram with transects, plots, and a dotted line indicating the location of the *Larrea* canopy drip line. UC = Under Canopy; CD = Canopy Drip line; ON = Open Near shrub; OF = Open Far from shrub (a). Transect diagram with plot sizes and distances between plots within a transect. The dotted line indicates the location of the canopy drip line. * Indicates that the distance between the UC and CD plots was variable and depended on the shrub canopy length in the transect direction (b).

conducted 4–12 November, 2010; this census began 15 days after the most recent rainfall event (11 mm) and after 17.3 mm of total recorded rainfall. The Mojave reproductive census was conducted 23 March through 3 April, 2011, after 131.1 mm of rainfall since the seedling census (Fig. 2a). In the Sonoran site, the seedling census was conducted 21–24 January, 2011; this census began 22 days after the most recent rainfall event (4 mm) and after 25 mm of total recorded rainfall. The Sonoran reproductive census was conducted 15–17 March, 2011, after 35 mm of rainfall since the seedling census (Fig. 2b). All individuals were classified as either native or non-native.

2.4. Statistical analysis

We summed the total number of native and non-native individuals per plot for each census in each desert. To avoid issues of pseudoreplication, we then summed these values across equivalent microhabitats of the two transects associated with each shrub since each pair has all factors in common. Count data such as these are discrete, have a high proportion of zeros and low values and have the property that the variance generally increases with the mean, and therefore can be viewed as generated from a Poisson process. Rather than apply transformations to make the data fit a linear model, we used a general linear model with a Poisson distribution because it fits the properties of our data (O’Hara and Kotze, 2010). Furthermore, because plant establishment is often spatially heterogeneous (Schabenberger and Pierce, 2002), the variance of the plant counts is often larger than the mean, or over-dispersed. Consequently, a simple Poisson distribution may not be adequate to describe the variation in our data. We addressed this issue by using an over-dispersed Poisson model, which is attained by defining the lowest level of observation as a random effect (McCarthy, 2007) and removes the requirement that all observations share the same Poisson distribution parameters. We used the GLIMMIX procedure in SAS software version 9.2 (2008) to fit a Poisson model with a log-link function. The response variable in the analysis was the summed plant counts. Shrub was treated as a random effect, whereas desert (Mojave or Sonoran), direction (North or South), microhabitat (UC, CD, ON, or OF), census (Seedling

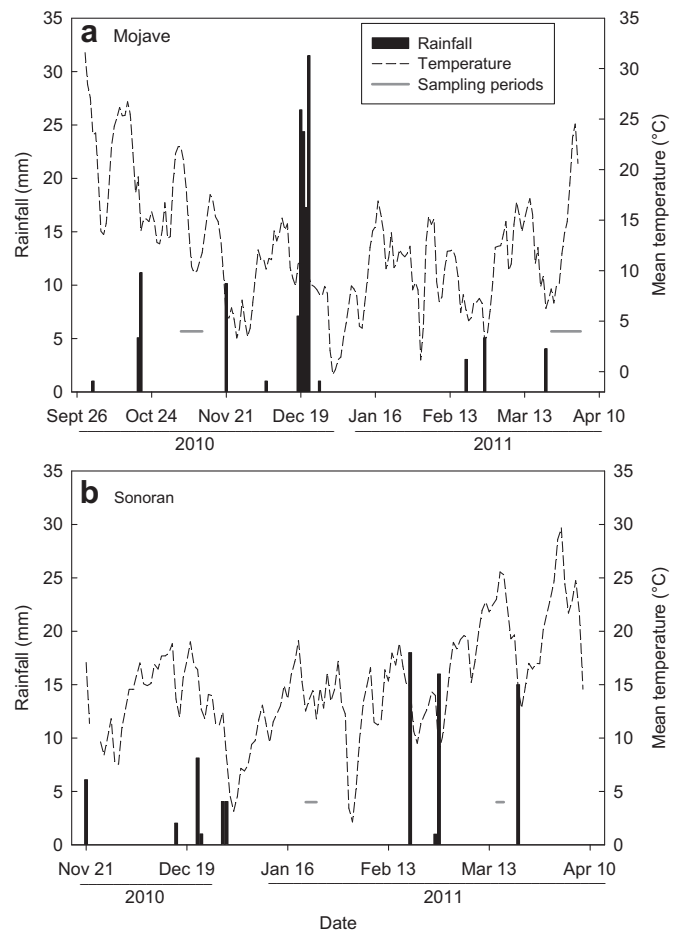


Fig. 2. Total daily rainfall, mean daily temperature, and the dates of the seedling and reproductive censuses in our Mojave Desert (a) and Sonoran Desert (b) study sites.

or Reproductive) and provenance (Native or Non-native) were all treated as fixed effects. The experimental design was nested at several levels. Shrub was nested within desert and direction, microhabitat was nested within shrub, and census and provenance were nested within microhabitat. We fit the lowest level of observation, census \times provenance, as a random effect nested within microhabitat to allow for over-dispersed values in the expected counts. We also fit all higher-order interactions of these effects. The Tukey–Kramer method was used to adjust p -values for multiple comparisons to keep $\alpha = 0.05$ when comparing pairwise differences.

3. Results

The abundance of annuals was approximately 10-fold higher in the Mojave Desert than in the Sonoran Desert (Table 1; desert term $F_{1,332} = 971.90, P < 0.0001$; see appendix Table A.1 for a list of native and non-native annual species encountered in our study plots) due to higher abundance of non-natives in the Mojave Desert; the number of native annuals was of the same order of magnitude in both deserts (Fig. 3). Differences in the relative abundance of natives and non-natives between the two censuses were not consistent between the two deserts (Table 2). In the Mojave Desert, the relative number of natives was lower in the seedling census (9.7%) than in the reproductive census (11.7%). In the Sonoran Desert, the pattern was reversed; 77.4% and 52.9% of the individuals counted in the seedling and reproductive censuses, respectively, were native species. In both deserts, there were more annuals on the north side of *Larrea* than on the south side of *Larrea* (Table 3),

Table 1
Type III tests of fixed effects for the over-dispersed poisson model fit to plant counts. Degrees of freedom (df) are listed as numerator, denominator.

Effect	df	F	P
Desert ^a	1,332	971.90	<0.0001
Direction ^b	1,332	62.68	<0.0001
Desert*Direction	1,332	9.35	0.0024
Microhabitat ^c	3,996	205.01	<0.0001
Desert*Microhabitat	3,996	3.63	0.0127
Direction*Microhabitat	3,996	28.68	<0.0001
Desert*Direction*Microhabitat	3,996	18.56	<0.0001
Provenance ^d	1,3984	1148.89	<0.0001
Desert*Provenance	1,3984	3433.33	<0.0001
Direction*Provenance	1,3984	56.94	<0.0001
Desert*Direction*Provenance	1,3984	59.89	<0.0001
Provenance*Microhabitat	3,3984	18.24	<0.0001
Desert*Provenance*Microhabitat	3,3984	128.90	<0.0001
Direction*Provenance*Microhabitat	3,3984	11.09	<0.0001
Desert*Direction*Provenance*Microhabitat	3,3984	11.86	<0.0001
Census ^e	1,3984	0.07	0.7938
Desert*Census	1,3984	0.02	0.8907
Direction*Census	1,3984	0.92	0.3387
Desert*Direction*Census	1,3984	166.85	<0.0001
Microhabitat*Census	3,3984	99.26	<0.0001
Desert*Microhabitat*Census	3,3984	6.74	0.0002
Direction*Microhabitat*Census	3,3984	1.70	0.1638
Desert*Direction*Microhabitat*Census	3,3984	55.86	<0.0001
Provenance*Census	1,3984	24.83	<0.0001
Desert*Provenance*Census	1,3984	109.18	<0.0001
Direction*Provenance*Census	1,3984	2.60	0.1071
Desert*Direction*Provenance*Census	1,3984	0.05	0.8209
Provenance*Microhabitat*Census	3,3984	0.51	0.6747
Desert*Provenance*Microhabitat*Census	3,3984	0.63	0.5979
Direction*Provenance*Microhabitat*Census	3,3984	0.42	0.7366
Desert*Direction*Provenance*Microhabitat*Census	3,3984	1.07	0.3588

^a Mojave, Sonoran.

^b north, south.

^c under canopy, canopy drip line, open near shrub, open far from shrub.

^d native, non-native.

^e seedling, reproductive.

and annuals were generally more abundant in the microhabitats not influenced by shrubs (ON and OF; Table 4).

In the Mojave Desert, abundance of native annuals on the north side of *Larrea* increased from under the canopy (close to the shrub stems) to the canopy drip line (UC vs. CD; seedling: $t = -6.57, P < 0.0001$; reproductive: $t = -6.18, P < 0.0001$; $df = 3984$ for all pairwise comparisons) then decreased in the open microhabitats (Fig. 3a,b). On the south side of *Larrea*, native annual abundance increased from under the canopy into the open far from the shrub in the seedling census (UC vs. OF: $t = -11.84, P < 0.0001$), but there was no difference among microhabitats in the reproductive census ($P > 0.05$ for all pairwise comparisons). Abundance of non-native annuals increased from under the canopy into the open, near shrub microhabitat and was similar between the ON and OF plots on both sides of *Larrea* in both censuses (Fig. 3a,b).

In the Sonoran Desert seedling census, abundance of native annuals on both sides of *Larrea* increased from under the canopy (close to the shrub stems) to the canopy drip line (UC vs. CD; north: $t = -9.71, P < 0.0001$; south: $t = -9.18, P < 0.0001$) and increased slightly from the canopy drip line into the open, near shrub microhabitat, then decreased or leveled off (Fig. 3c). In the reproductive census, abundance of native annuals was higher in the open microhabitats than under the canopy (e.g. UC vs. ON: $t = -6.27, P < 0.0001$) on the south side of *Larrea* and did not differ significantly among microhabitats on the north side of *Larrea* (Fig. 3d). The abundance of non-native annuals in the Sonoran seedling census tended to be higher at the canopy drip line than under the canopy on both sides of *Larrea* (UC vs. CD; north: $t = -5.08, P = 0.0007$; south: $t = -4.05, P = 0.061$) and was similar among the CD, ON and OF plots (Fig. 3c). In the reproductive census, however, abundance of non-native annuals was higher in the open microhabitats than in the shrub-associated microhabitats on the south side of *Larrea* and decreased from under the canopy (close to the shrub stems) into the open, near shrub microhabitat (UC vs. ON: $t = 4.41, P = 0.015$) on the north side of *Larrea* (Fig. 3d). Abundance of non-natives in the open microhabitats was similar on the north and south sides of *Larrea* (ON: $t = 0.33, P = 1$; OF: $t = 1.90, P = 1$).

Interactions between direction, provenance of annual plants, and the time of the census were most evident under the canopy (UC microhabitat). In the seedling census in the Mojave Desert, there were more native and non-native annuals under the north than south side of *Larrea* (natives: $t = 12.55, P < 0.0001$; non-natives: $t = 10.81, P < 0.0001$). In the reproductive census, however, there was no effect of direction on the abundance of native and non-native annuals in the UC microhabitat (natives: $t = 1.82, P = 1$; non-natives: $t = 0.53, P = 1$) due to a decrease and increase in the number of annuals under the north and south sides of *Larrea*, respectively (Fig. 3a,b). In the seedling census in the Sonoran Desert, the number of native and non-native annuals was similar under the north and south sides of *Larrea* (natives: $t = -1.38, P = 1$; non-natives: $t = -0.50, P = 1$). In the reproductive census, however, there were more native and non-native annuals under the canopy on the north side of *Larrea* (natives: $t = 5.72, P < 0.0001$; non-natives: $t = 6.49, P < 0.0001$) due to an increase in annuals in this microhabitat (Fig. 3c,d).

4. Discussion

In both the Mojave and Sonoran Deserts, abundance of annuals was higher on the north side of *Larrea*, particularly in the shrub-influenced microhabitats, as hypothesized. Soil nitrogen is generally higher under the north side of *Larrea* than under the south side of *Larrea* (Brooks, 1999a). Solar radiation and soil temperature are lower under shrubs than in the open (Forseth et al., 2001), and directional differences in shading have been shown to exist in arid

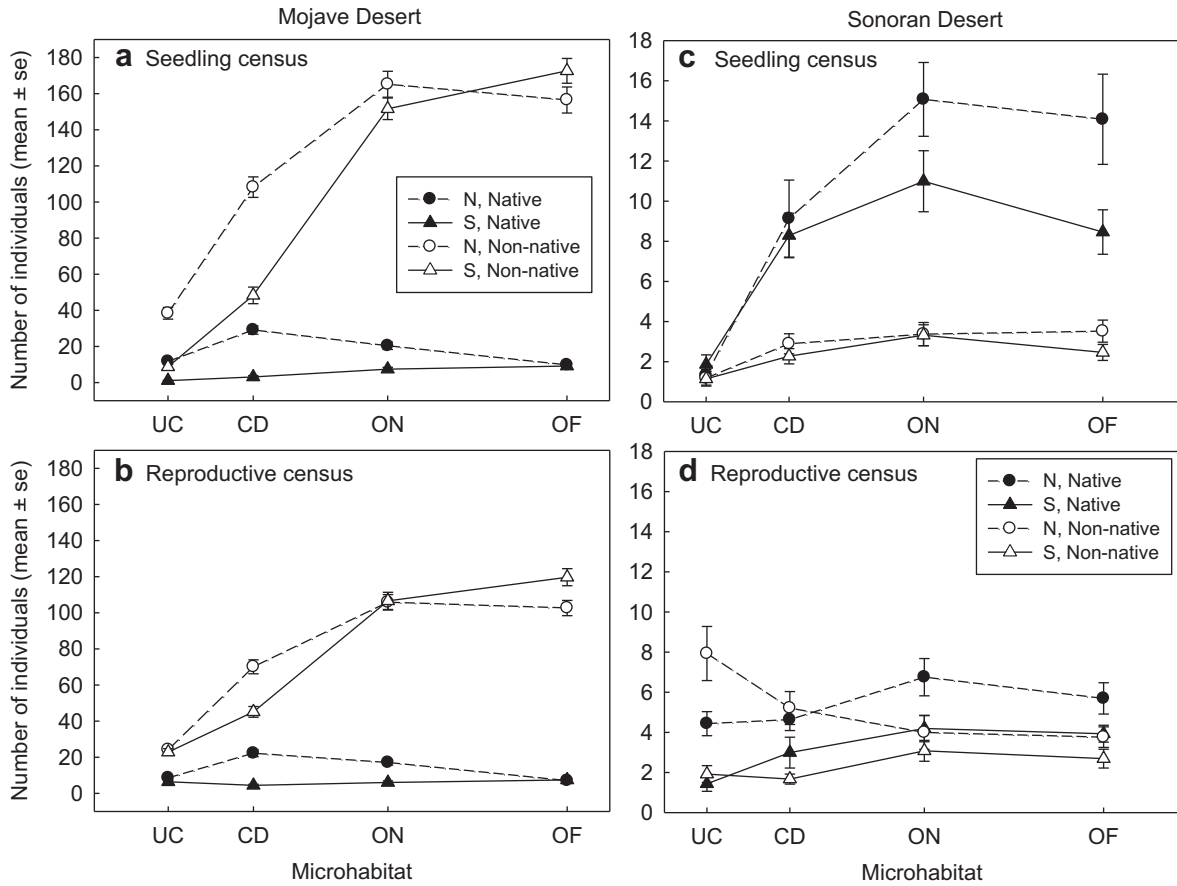


Fig. 3. Mean (± 1 se) number of native and non-native individuals in each microhabitat and direction (summed across equivalent microhabitats of the two transects associated with each shrub) for the seedling (a) and reproductive (b) censuses in the Mojave Desert and the seedling (c) and reproductive (d) censuses in the Sonoran Desert. The x-axis is scaled according to the distance between plots with the *Larrea* stem at zero. Note the differences in the scale of the y-axis between deserts.

systems (e.g. Schenk and Mahall, 2002; Valiente-Banuet and Ezcurra, 1991). Higher nitrogen availability and lower temperatures under the north, as compared to the south, side of *Larrea* likely facilitated the high abundance of annuals on the north side of *Larrea* that was observed in this study.

Despite positive directional effects of resource heterogeneity on annual plant abundances, *Larrea* appeared to have overall negative effects on annual abundances in our study. Contrary to our

hypothesis, the abundance of native annuals was highest at the canopy drip line and open near shrub microhabitats in the Mojave Desert and highest in the open microhabitats in the Sonoran Desert. In support of our hypothesis, the abundance of non-native annuals was highest in the open areas among shrubs in both of our desert sites. *Larrea* roots are concentrated in the upper soil horizons and extend into the open areas among shrubs (Garcia-Moya and McKell, 1970) and can have allelopathic effects on intra- and interspecific root growth (Mahall and Callaway, 1992), but nutrient availability is higher under shrubs than in the open (e.g. Charley and West, 1975; Ewing et al., 2007; Schlesinger et al., 1996; Thompson et al., 2005). Nutrient availability was similar in our Mojave and Sonoran sites,

Table 2

Effects of provenance and time of census on annual plant abundances in the Mojave and Sonoran Deserts. Least squares means of parameter estimates (x), determined in the general linear model, are given for each combination of fixed effects of desert, provenance, and census. Because the general linear model used a log-link function, parameter estimates (x) were transformed to expected counts for the plots as e^x . Expected counts with different letters are significantly different ($\alpha = 0.05$; adjusted for multiple comparisons using the Tukey–Kramer method). The letter A is next to the group with the largest expected count, B next to the next largest expected count, etc. Letters are spaced to aid in visual comparison.

Desert	Provenance	Census	Parameter estimate (x)	Expected count (e^x)
Mojave	Native	Seedling	1.72	5.61D
Mojave	Native	Reproductive	1.86	6.44C
Mojave	Non-native	Seedling	4.14	62.81 A
Mojave	Non-native	Reproductive	4.01	55.08B
Sonoran	Native	Seedling	1.23	3.42E
Sonoran	Native	Reproductive	0.86	2.37F
Sonoran	Non-native	Seedling	0.24	1.27H
Sonoran	Non-native	Reproductive	0.63	1.88G

Table 3

Effects of direction on annual plant abundances in the Mojave and Sonoran deserts. Least squares means of parameter estimates (x), determined in the general linear model, are given for each combination of fixed effects of desert and direction. Because the general linear model used a log-link function, parameter estimates (x) were transformed to expected counts for the plots as e^x . Expected counts with different letters are significantly different ($\alpha = 0.05$; adjusted for multiple comparisons using the Tukey–Kramer method). The letter A is next to the group with the largest expected count, B next to the next largest expected count, etc. Letters are spaced to aid in visual comparison.

Desert	Direction	Parameter estimate (x)	Expected count (e^x)
Mojave	N	3.32	27.66 A
Mojave	S	2.55	12.78 ...B
Sonoran	N	0.91	2.49C
Sonoran	S	0.57	1.77D

Table 4

Effects of microhabitat on annual plant abundances in the Mojave and Sonoran Deserts. Least squares means of parameter estimates (λ), determined in the general linear model, are given for each combination of fixed effects of desert and microhabitat. Because the general linear model used a log-link function, parameter estimates (λ) were transformed to expected counts for the plots as e^λ . Expected counts with different letters are significantly different ($\alpha = 0.05$; adjusted for multiple comparisons using the Tukey–Kramer method). The letter A is next to the group with the largest expected count, B next to the next largest expected count, etc. Letters are spaced to aid in visual comparison.

Desert	Microhabitat	Parameter estimate (λ)	Expected count (e^λ)
Mojave	UC ^a	2.08	7.97C
Mojave	CD ^b	2.93	18.84 ...B
Mojave	ON ^c	3.42	30.64 A
Mojave	OF ^d	3.30	27.16 A
Sonoran	UC	0.06	1.07F
Sonoran	CD	0.78	2.19E
Sonoran	ON	1.09	2.99D
Sonoran	OF	1.02	2.79D

^a Under canopy.

^b Canopy drip line.

^c Open, near shrub.

^d Open, far from shrub.

and nitrogen and potassium availability tended to be higher under shrubs than in the open (E. Mudrak, unpublished data). Greater abundance of annuals away from the shrub canopy suggests that negative effects of *Larrea* competition or allelopathy are stronger than the positive effects of *Larrea* fertility islands in our study sites. Furthermore, lower abundance of annuals under the shrub canopy close to the shrub stems compared to at the canopy drip line indicates that negative effects of *Larrea* are greater near the base of *Larrea* individuals, possibly due to differences in root biomass between these microhabitats (Callaway et al., 1991).

Although many studies have predicted that more severe environmental conditions will cause shrub effects to shift from negative to positive (e.g. Bertness and Callaway, 1994; Callaway and Walker, 1997; Holmgren et al., 1997), a study by Tielbörger and Kadmon (2000) found that shrubs had a more positive effect on annual plant densities during years with high rainfall in the Negev Desert. In our study, an increase in annual plant abundances in the shrub-influenced microhabitats between the seedling and reproductive censuses suggests that the negative effects of *Larrea* weakened over the winter growing season. We suspect that this is related to rainfall and the effects of soil moisture on *Larrea* competition, nutrient availability, and seed germination. Because *Larrea* growth is water limited and does not appear to be nitrogen limited (Sharifi et al., 1988), an increase in rainfall likely decreases competition between *Larrea* and annuals. Furthermore, nitrogen availability is positively correlated with precipitation to a greater degree in shrub patches than in the open (Schade and Hobbie, 2005), and increased nutrient availability has a positive effect on the density of non-native species (Brooks, 2003). An increase in the abundance of non-native annuals under the south side of *Larrea* in our Mojave site and an increase in overall annual abundance under both sides of *Larrea* (but the increase was greater on the north side) in our Sonoran site indicate additional germination events between the seedling and reproductive censuses. Furthermore, this suggests that the effects of rainfall on germination may differ between native and non-native species and depend on directional differences. In our Mojave site, only 9 mm of rain fell in the month before the reproductive census, and this rainfall seems to have stimulated germination of non-natives more so than natives. Gutiérrez (1992) found that water addition increased biomass of non-native species but not native species, suggesting that non-native species are better competitors or have lower moisture thresholds for germination and growth. In our Sonoran site, more than half of the total rain fell in

the month before the reproductive census, and this rainfall had a greater effect on germination under the north side of *Larrea*, possibly due to synergistic effects of soil moisture, nutrient availability (Brooks, 1999a), and temperature (Forseth et al., 2001). Differential effects of soil moisture depending on species provenance and shrub direction could have important consequences for the abundance and distribution of native and non-native species.

We assessed annual abundances in only one site in the Mojave and Sonoran Deserts, but it is worth noting that the abundance patterns of non-natives in the Mojave were similar to the abundance patterns of natives in the Sonoran. Variation in factors affecting the invasibility of the two deserts (Brooks and Chambers, 2011), such as historical factors (e.g. patterns of introduction of non-native species and differences in propagule pressure), dispersal of non-native species, soil characteristics, overall aridity, or rainfall patterns could contribute to a much higher proportion of natives (~65% vs. ~11%) in the Sonoran Desert, which could affect annual abundance patterns. Alternatively, the differences between deserts could be specific to years with weather similar to that in our study year. During the period we recorded rainfall, our Mojave and Sonoran sites received 148 mm and 60 mm of rainfall, respectively, which is average for our Mojave site and below average (61% lower) for our Sonoran site. There can be large inter-annual variation in density and species richness of desert annuals (Bowers, 1987; Guo et al., 2002), and the non-native annual *Erodium cicutarium* has a negative effect on native annuals only during years when it reaches high densities (Schutzenhofer and Valone, 2006). Long-term studies in multiple sites are needed to determine if the differences in annual plant abundance patterns between the Mojave and Sonoran Deserts observed in this study are consistent across sites and among years with different rainfall amounts.

We found that *Larrea* seems to have overall negative effects on the abundance of annuals, regardless of provenance, unlike the desert shrub *A. dumosa*, which has facilitative effects on annuals (Holzapfel and Mahall, 1999); this difference could be related to the fact that *Larrea* is allelopathic and *A. dumosa* is not (Mahall and Callaway, 1992). Negative and positive effects of shrubs can occur at the same time (e.g. Callaway, 1994; Facelli and Temby, 2002; Holmgren et al., 1997; Holzapfel and Mahall, 1999), and the balance of positive versus negative effects of *Larrea* appears to depend on environmental factors that vary with respect to direction. In addition, the importance of facilitative versus competitive effects of shrubs depends on the intensity of abiotic stress (Bertness and Callaway, 1994), and our results suggest that the intensity of abiotic stress under *Larrea* varies during the winter growing season in the Mojave and Sonoran Deserts. Differences in abiotic stress over the growing season may be related to size-specific interactions (Morris and Wood, 1989) or changes in resource availability. Furthermore, differences among site factors such as rainfall, soil characteristics, and species composition – either within or among deserts – likely influences interactions between *Larrea* and annuals. Further knowledge of the effects of *Larrea*, which is a dominant species throughout the southwestern United States, on abundances of native and non-native annuals is necessary to gain a better understanding of the dynamics of species interactions in desert scrub ecosystems.

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Appendix A. Supplementary data

Supplementary data related to this article can be found online at <http://dx.doi.org/10.1016/j.jaridenv.2012.07.013>.

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