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Biting the hand that feeds: the invasive grass *Schismus barbatus* (Poaceae) is facilitated by, but reduces establishment of, the native shrub *Ambrosia dumosa* (Asteraceae)

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Abstract

Question: We present a study of positive and negative interactions between the invasive grass *Schismus barbatus* (Poaceae) and *Ambrosia dumosa* (Asteraceae). *Ambrosia* facilitates seedling establishment, and such facilitation may accelerate invasion of exotic species, which, in turn, may reduce establishment of native plants.

Location: Joshua Tree National Park, California, USA.

Methods: During 2003-2004, we used field surveys to characterize the natural spatial distribution of *Schismus* in relation to native shrubs, and experimentally manipulated seed rain of *Ambrosia* and *Schismus* at three distances from adult *Ambrosia* canopies. We measured percentage germination and individual performance of both species. Field data were complemented by a greenhouse experiment that measured competition between *Ambrosia* seedlings and *Schismus* planted at three densities and five relative abundances under controlled conditions.

Results: Field surveys showed that the density of *Schismus* is independent of *Ambrosia* shrubs, but growth is enhanced near shrub canopies. In our field experiment *Schismus* is facilitated by adult *Ambrosia*. Under controlled conditions, *Schismus* does not respond to the density of *Ambrosia* seedlings, but changes in density of *Schismus* decreased performance of *Ambrosia* seedlings.

Conclusion: *Schismus* invasion may be detrimental to native perennial plant populations. Although a reduction of seedling establishment is not usually expected to slow population growth of long-lived perennials, recent unprecedented adult mortality in this community, and the well-documented facilitative role of *Ambrosia*, suggest that *Schismus* invasion may be of high ecological significance.

Keywords: Population ecology; Desert; Island of fertility; Competition; Facilitation; Seedling survival.

Nomenclature: Anon. (2009).

Introduction

Invasive grasses have changed the composition and functioning of western arid ecosystems in the United States. Notable among these is the Mediterranean grass *Schismus barbatus* (Loefl. ex L.) Thellung, which is one of the most abundant and widespread exotic species in the Mohave and Sonoran Deserts (Brooks 1999; Brooks & Berry 2006). Native to Eurasia, *Schismus* was first reported in central California (Hoover 1936) and has since become widely distributed in US southwestern deserts (Brooks 1999; Brooks & Berry 2006). *Schismus* abundance is negatively correlated with abundance and diversity of native annuals (Brooks 2000), reflecting, in part, the ability of this grass to grow at very high densities (up to approx. 10 000 plants m^{-2}; Venable 2007) and dominate areas with a high-nitrogen content (Brooks 2003). Most damaging among the documented impacts of *Schismus* is its positive association with increases in fire frequency (Brooks & Pyke 2001; Brooks & Berry 2006).

To date, little is known about the relative frequency of competitive and facilitative interactions between *Schismus* and perennial shrubs. In general, perennials create spatial heterogeneity that promotes coincident establishment and growth of annual and perennial seedlings (Tielbörger & Kadmon 1995; Facelli & Temby 2002; Holzapfel et al. 2006). In contrast to inter-shrub spaces, areas close to shrubs serve as "resource islands" (Schlesinger & Pilmanis 1998) because they are nutrient-rich (Schlesinger et al. 1996; Facelli & Temby 2002; Titus et al. 2002), have favorable soil properties, higher water availability, and reduced irradiance (Forseth et al. 2001). These conditions promote denser and more diverse assemblages of annuals under shrubs than in inter-shrub spaces (Tielbörger & Kadmon 1995; Facelli & Temby 2002; Holzapfel et al. 2006). However, when very high densities of annuals and juvenile perennials co-occur, interspecific competition may override positive effects of such resource islands (Holzapfel & Mahall 1999; Forseth et al. 2001; Maestre et al. 2003; Miriti 2006). A net positive effect of shrubs on annuals, in general, and on *Schismus*, in particular, occurs when the benefits of shrub proximity offset the negative effects of competition.

The collective effect of annuals may reduce establishment and survival of perennial shrubs that facilitate the annual community. A dense annual community exacerbates water stress under the perennial canopies (Holzapfel & Mahall 1999) and may reduce successful establishment of perennial seedlings. Perennial seedlings must overcome water and nutrient limitations under intense competition, which is particularly challenging since establishing perennials typically have lower water-use efficiency than annuals, and young perennials have incipient root systems (Sandquist et al. 1993; Housman et al. 2003). Thus, *Schismus* success may be contingent on the predominant interactions with established shrubs. In contrast, shrub recruitment may depend on the strength and widespread distribution of *Schismus* success.

Our aim is to assess the importance of bur-sage, *Ambrosia dumosa* (Gray) Payne, on the maintenance of *Schismus* populations and to evaluate the impact of *Schismus* on the survival and growth of *Ambrosia* seedlings. *Ambrosia dumosa* is one of the most abundant shrubs in the Sonoran and Mohave Deserts (Turner et al. 1995) and changes in *Ambrosia* abundance are likely to influence the creation and maintenance of resource islands in communities where *Ambrosia* is dominant. Therefore, our results contribute to comprehensive assessment of the impact of invasive grasses in desert ecosystems.

Using field surveys and experiments, we addressed three questions: 1) What is the spatial distribution of *Schismus* in a community dominated by *Ambrosia*? 2) How do germination and growth of *Schismus* and *Ambrosia* seedlings vary in microhabitats defined by the presence of, and distance from, adult *Ambrosia* plants? 3) What is the outcome of competition between *Schismus* and *Ambrosia* seedlings when both species are grown at a range of densities and relative abundances?

We expect to find differences in the establishment, growth and survival of *Schismus* within microhabitats defined by the proximity to adult *Ambrosia*. Consequently, we expect that population persistence of *Schismus* depends on individual performance within these distinct microhabitats, and that the spatial distribution of *Schismus* shows a clear signature of this differential performance. Finally, we expect *Schismus* to directly modify *Ambrosia* population trajectories by diminishing successful recruitment of *Ambrosia* seedlings.

Methods

Study system

The study was undertaken in Joshua Tree National Park, California (33°44′761″N-115°48′717″W; elevation 1006 m) on a gently sloping bajada ($\leq 4\%$) to the southwest of the Eagle Mountains, approximately 1.4 km north of Cottonwood Spring. Rainfall typically occurs between September and March, and averaged 11.9 cm year^{-1} at Twenty-nine Palms Station from 1980 to 2004 (National Climatic Data Center). In addition to *Ambrosia dumosa*, the most abundant species within the study site are Creosotebush (*Larrea tridentata* Coville) and Hall's purple bush (*Tetracoccus hallii* Brandeg).

Ambrosia dumosa is a monoecious, drought-deciduous shrub between 20 and 60 cm in height. *Ambrosia* acts as nurse plant for several annual species that grow at higher densities (Schenk et al. 2003) and have higher biomass and seed production below the *Ambrosia* canopy (Holzapfel & Mahall 1999).

Spatial distribution of Schismus

Heterogeneity in edaphic factors and unique responses of *Schismus* to individual shrub species may influence the spatial distribution of *Schismus*. We conducted a field survey in March 2004 within a 1 ha area to (1) measure spatial heterogeneity in the local density of *Schismus* and (2) measure spatial dependence of *Schismus* performance in response to distance from native perennials. This hectare site contains a group of well-studied shrubs and cacti that represent the diversity of perennials that occur in the region and has been free of human disturbance for more than 70 years (Miriti et al. 1998). The hectare site was divided into 20 parallel transects of 100 m in length. We sampled an area 15 cm in diameter every 5 m along these transects, resulting in a total of 441 sampling units.

At each sampling unit, we recorded *Schismus* density, the distance and orientation to the closest adult shrub, and the identity of the nearest shrub species. We also measured the height of *Schismus* for a subsample of ten individuals per sampling point. At every 10 m along each transect, we harvested the complete aboveground biomass of annuals. After measuring dry biomass of all collected plants, the material was sorted to isolate *Schismus* biomass.

To achieve the first objective of evaluating heterogeneity of *Schismus* at local scales, we used correlogram analysis to measure the correlation between *Schismus* density and the distance between sampling units. For this analysis, we used the density measures taken at 5-m intervals. Significant correlation in density among paired sampling units within a given distance interval indicates that sampling points are autocorrelated and cannot be considered independent. Such a result suggests that those points share characteristics that promote consistent variation of density in the same (positive) or opposite (negative) direction. Moran's I (Perry et al. 2002) was used to determine the significance of observed spatial autocorrelation. This statistic ranges from 1 to -1, with 1 indicating a strong positive spatial autocorrelation and -1 a strong negative autocorrelation. These analyses were conducted using Passage (Rosenberg 2001).

Our sampling protocol permitted us to test two categories of *Schismus* response to native shrubs. The initial question was whether *Schismus* performance was sensitive to distance from native shrubs. This was tested using multivariate linear regression with *Schismus* density, height, and biomass as response variables, and with distance to the nearest perennial, volume of the nearest perennial, and the biomass of all non-*Schismus* plants as explanatory variables. We calculated the volume of perennials following Miriti et al. (2001). As a separate analysis, our sampling points could be grouped into three distinct microhabitats defined by shrub canopies: (1) below the canopy of a focal shrub, (2) at the border of a focal shrub, and (3) in open, inter-shrub areas. We used generalized linear models to compare *Schismus* density in response to these shrub canopy effects. Because data points were collected along a regular grid rather than randomly, we tested for spatial independence of our performance measures among the sampling units using Moran's I. When we found spatial autocorrelation, we used spatial variate differencing (Cliff & Ord 1981) to filter the data. In addition, we used log-transformed response variables to fulfill normality and homocedasticity requirements.

Effects of adult Ambrosia plants on Ambrosia seedlings and Schismus

We conducted a field experiment to test the hypothesis that *Schismus* and *Ambrosia* seedlings experience enhanced growth when they occur close to established *Ambrosia* adults. In October 2003, we randomly selected 20 *Ambrosia* adults from the study area. Three distance categories were established: (1) at the canopy edge, (2) between 100 and 150 cm, and (3) between 150 and 200 cm. Paired sections of PVC pipe 15 cm in diameter and 30 cm high were buried in the ground along the E-W axis of each shrub at each distance. The purpose of these pipes was to minimize the effects of intrinsic variation in seed distribution along our distance gradient. Five grams of *Schismus* (101 973 seeds, SE = 394.02) and 2 g of *Ambrosia* seeds (167 seeds SE = 8.95) were mixed within the top 5 cm of soil from one of each pair of pipes. The second pipe was used as a control, with no seed addition. In March 2004, after *Schismus* has reproduced and before seed dispersal, we estimated the density of both species in each pipe and harvested all aboveground biomass. Finally, we measured height and dry weight of a sub-sample of ten *Schismus* from each pipe.

To analyze the effects of distance and seed addition on *Schismus* height and weight, we used generalized linear models, with distance and seed addition as fixed factors, and biomass of non-target species as covariate. We included density as a covariate in our analyses of individual average height and weight. Multiple comparisons of distance and treatment were performed using Tukey's simultaneous comparisons. Response variables were log-transformed to fulfill normality and homoscedasticity requirements.

Competition between Schismus and Ambrosia seedlings

We conducted a surface response experiment (Gibson et al. 1999) to test the hypothesis that *Schismus* and *Ambrosia* seedlings compete. A surface response experiment consists of a group of replacement series experiments in which competing species are grown at different frequencies while total density is kept constant. This experiment was conducted during the winter of 2004 in the Biological Sciences greenhouse at Ohio State University. We used three replacement series, each at one of three total densities. At each total density, seedlings of *Ambrosia* and *Schismus* were grown at five relative abundances for a total of 15 different treatment combinations (Table 1). Each treatment was

Table 1. Set up of the greenhouse surface response experiment for seedlings of *Schismus barbatus* (SB) and *Ambrosia dumosa* (AD). Each cell represents a treatment combination. Given initial seedling biomass differences, ten plants of *Schismus* were considered equivalent to one seedlings of *Ambrosia*. Numbers in parenthesis indicates density of *Schismus* in 1 m^2. Each treatment combination was replicated four times.

	Total density					
	Low (4 individual pot^{-1})		Medium (8 individual pot^{-1})		High (16 individual pot^{-1})	
% of AD	AD	SB	AD	SB	AD	SB
100%	4	0	8	0	16	0
75%	3	10 (137)	6	20	12	40
50%	2	20 (274)	4	40	8	80
25%	1	30 (411)	2	60 (822)	4	120 (1694)
0%	0	40 (548)	0	80 (1096)	0	160 (2193)

replicated four times. Plants were grown in 14.5 L containers (30 cm in diameter) using a (3:1) mixture of sand and perlite. The soil mixture was fertilized with 2.8 g pot^{-1} of Osmocote 14/14/14 (N/P/K) at the beginning of the experiment. Treatments were randomly assigned to each of the 60 containers.

At the beginning of the experiment, a mixture of seeds of both species was sown homogeneously in each container. In order to compensate for differences in seedling biomass between target species, ten plants of *Schismus* were considered equivalent to one *Ambrosia* plant. We thinned seedlings to target densities 2 weeks after germination. Irrigation, temperature, and light were controlled to match values in the field during the growing season of 2003. We used precipitation and temperature data from the Twenty-nine Palms Meteorological Station (National Climatic Data Center).

Height of both species was measured at the beginning of the experiment (initial height), at the end of the first month, and after 3.5 months, when *Schismus* flowered. Aboveground biomass was measured at the beginning and at the end of the experiment when *Schismus* produced flowers. For a sub-sample of five *Schismus* per container, we counted the number of seeds per plant. We used a two-way ANOVA to compare relative growth in height and biomass of *Ambrosia* and *Schismus* plants among treatment combinations, and Turkey's simultaneous comparisons to conduct multiple comparisons. Multivariate regression models were used to analyze the relationship between densities of both species on growth variables. Response variables were transformed when necessary to fulfill normality and homocedasticity assumptions.

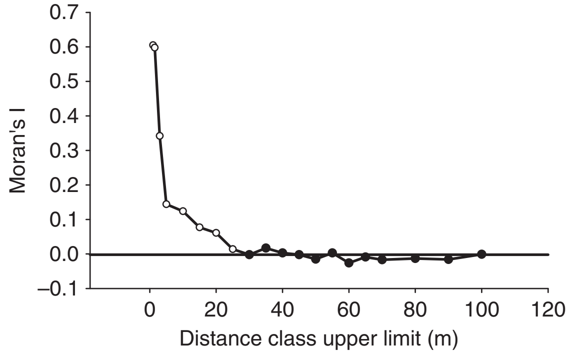

Fig. 1. Moran's I function describing the correlation between *Schismus barbatus* density and distance between sampling units taken from transects within 1 ha at JTNP during 2004. Open circles designate significant ($\alpha = 0.05$) positive correlation in density among points within the distances given on the *x*-axis compared to a random distribution.

Results

Natural distribution of Schismus

Spatial autocorrelation in Schismus distribution

Seventy-seven per cent of the samples taken within the 1 ha area included *Schismus*. Density ranged from one to 200 plants sample^{-1} unit (mean = 23.51, SD = 28.293 $n = 335$). *Schismus* density showed significant positive spatial autocorrelation (Fig. 1). Moran's I was significant overall, declining with distance up to 20-25 m.

Spatial dependence of Schismus performance

After correcting for spatial autocorrelation, multivariate linear regression showed that proximity to shrub canopies significantly enhanced *Schismus* performance, with individual plants being heavier and significantly taller close to shrub canopies (Table 2). Although average aboveground biomass decreased with both distance from shrubs and size of shrubs, these trends were not significant. Similarly, we did not detect a significant effect of distance from a shrub on *Schismus* density. In fact, the generalized linear model showed that despite an apparent trend (canopy border: 1692 plants m^{-2}, SD = 33.86, $n = 20$; open: 868 plants m^{-2}, SD = 25.27, $n = 101$; below canopy: 758 plants m^{-2}, SD = 23.56, $n = 20$), *Schismus* density did not significantly vary with position relative to shrub canopies ($F = 1.51$ $P = 0.223$).

Field experiment: effect of adult Ambrosia plants on seedling performance

Overall, seed germination under no manipulation field conditions was low. No *Ambrosia* seedlings

Table 2. Multivariate linear regression using *Schismus* growth variables measured in natural populations. Estimated coefficients are indicated for each variable with their associated *P*-value in parenthesis. All variables were log-transformed to meet normality.

Response variable	N	R^2	Constant	Distance to the closest shrub	Biomass other species (mg)	Volume of closest shrub (cm^3)	Density of *Schismus* indv pipe^{-1})
Density (indvidual pipe^{-1})	98	2.9	0.626 (<0.001)	−0.001 (0.430)	0.015 (0.846)	-1.00×10^{-6} (0.112)	–
Total biomass (mg)	94	6.1	−0.223 (0.171)	−0.004 (0.048)	−0.122 (0.214)	-1.2×10^{-6} (0.172)	–
Individual height (cm)	93	10.7	1.601 (<0.001)	−0.001 (0.009)	0.020 (0.567)	-1.7×10^{-7} (0.461)	0.001 (0.045)
Individual biomass (mg)	96	31	−0.633 (<0.001)	−0.004 (0.021)	−0.054 (0.525)	-8.9×10^{-7} (0.250)	0.0136 (<0.0001)

germinated during our field experiment and the percentage germination of *Schismus* averaged only 0.026% of seeds sown (95% CI = [0.01, 0.04], n = 59). *Schismus* density was 1938.1 plants m^{-2} (SD = 2384.7) in control pipes and 3384.2 plants m^{-2} (SD = 4084.1) in pipes with seed addition.

In contrast to our results from the field survey, we detected a clear effect of distance from *Ambrosia* canopies on *Schismus* density. *Schismus* density in treatment pipes was significantly higher at intermediate and large distances than close to *Ambrosia* (P value$_{\text{canopy versus intermediate}} = 0.011$; P value$_{\text{canopy versus open}} = 0.0008$), while it did not significantly change with distance in control pipes. In agreement with the pattern observed in natural populations, we found that *Schismus* height and biomass were greater for plants occurring close to *Ambrosia* canopies (Fig. 2). Height significantly decreased as distance and density increased, while biomass decreased with distance and significantly decreased with density. These patterns were not significantly affected by biomass of non-target species (Table 3).

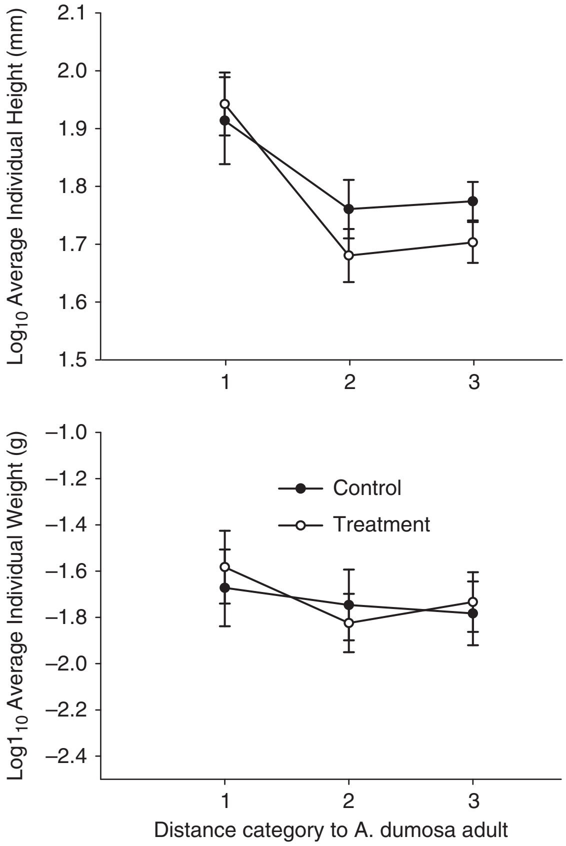

Fig. 2. Average individual height and biomass of *Schismus* measured during the field experiments. Paired PVC pipes were buried at three distances from the center of adult *Ambrosia* plants. A mixture of *Schismus* and *Ambrosia* seeds was sown into one of each pair of pipes (treatment); the other pipe was used as control. Averages were calculated using a subsample of ten *Schismus* plants from each pipe.

Greenhouse experiment: competition between Schismus and Ambrosia seedlings

During the greenhouse experiment, seedlings of *Ambrosia* responded more than seedlings of *Schismus* to changes in total density and relative abundance of both species. Seedlings of *Ambrosia* grew a maximum of 4.5-times the initial height and 105-times the initial weight (average final height = 11.6 cm, SD = 5.9, n = 278; average final dry weight = 156.5 mg, SD = 180.8, n = 280). Increases in height and biomass declined as total density increased (Table 4). This pattern was consistent across treatments independent of the relative abundance of *Ambrosia* (two-way ANOVA, density: $p<0.0001$, proportion of *Ambrosia*: $P>0.05$, interaction: $P>0.05$). Thus, *Ambrosia* responds to density and not species identity, the inference being an equivalent competitive effect of both species.

In contrast, *Schismus* grew a maximum of 18.6-times the initial height and up to 116.5-times the initial weight (average final height = 9.1 cm, SD =

Table 3. Generalized linear model results from field experiment. Variables were measured on *Schismus* plants growing in PVC pipes located at three distances from adult *Ambrosia* shrubs. Treatment refers to ± addition of a seed mixture of *Ambrosia* and *Schismus*. *P*-value for each factor is indicated, together with R^2 of the model. All variables were log-transformed to meet normality, and refer to *Schismus* unless otherwise indicated.

	N	Model R^2	Distance to shrub	Seed treatment	Distance× treatment	Biomass other species (mg)	Density (Individual pipe^{-1})
Density (individual pipe^{-1})	118	23.18	0.001	0.010	0.024	0.598	
Total biomass (mg)	118	10.4	0.032	0.013	0.084	0.522	
Individual height (cm)	115	45.31	<0.0001	0.216	0.111	0.430	0.038
Individual biomass (mg)	115	17.51	0.193	0.328	0.546	0.335	<0.0001

Table 4. Multivariate regression analysis for growth variables measured during the greenhouse response surface experiments. Variables indicate growth over 3.5 months. Each variable was regressed against density of *Schismus* and density of *Ambrosia*. *P*-value for each factor is indicated, together with R^2 of the model. All variables were log-transformed to meet normality.

Growth Variable	*N*	Model R^2	Density SB	Density AD
Height (cm) of *Ambrosia*	46	53.4	−0.064 (<0.001)	−0.044 (<0.001)
Biomass (mg) of *Ambrosia*	46	28.5	−0.111 (0.003)	−0.097 (0.002)
Height (cm) of *Schismus*	47	20.5	−0.047 (0.011)	−0.062 (0.008)
Biomass (mg) of *Schismus*	47	2.3	0.0053 (0.822)	−0.0168 (0.365)

4.25, $n = 1115$; average final dry weight = 26 mg, SD = 41, $n = 280$). Growth in biomass was not affected by total density in general, or by densities of *Schismus* or *Ambrosia* in particular (Table 4). However, *Schismus* biomass significantly differed with the relative abundance of *Ambrosia* (two-way ANOVA, proportion of *Ambrosia*: $P = 0.005$, density: $P = 0.405$, interaction: $P = 0.390$). These differences are mostly due to the contrasting growth between treatments, with 50 and 75% of *Ambrosia* ($\text{Difference}_{50-75\%} = 0.5658$, *t*-value = 3.826, $P = 0.0023$) and suggest distinct inter- and intraspecific competitive effects. On the other hand, growth in height decreased with total density but did not change with the relative abundance of *Ambrosia* or the interaction between these factors (two-way ANOVA, density: $P = 0.003$, proportion *Ambrosia* $P = 0.519$, interaction: $P = 0.362$). Increases in height decreased with increasing density of both *Ambrosia* and *Schismus* (Table 4).

Schismus plants devoted an average 43.6% of their biomass to reproduction, producing an average of 128.4 seeds individual^{-1} (SD = 143.82, $n = 240$). Both height and weight were good predictors for this variable ($Y = 3.99 + 0.0986$ Biomass, $R^2 = 82$, $p < 0.001$; $Y = -3.40 + 0.103$ Height, $R^2 = 58.5$, $p < 0.001$). Seed number did not respond to increases in total density (two-way ANOVA, density: $P = 0.208$, proportion of *Ambrosia* $P = 0.002$, interaction: $P = 0.391$). However, the proportion of biomass devoted to reproduction decreased with density, and was lowest when *Ambrosia* reached 50% abundance (two-way ANOVA, density: $P = 0.033$, proportion of *Ambrosia*: $P = 0.008$, interaction:

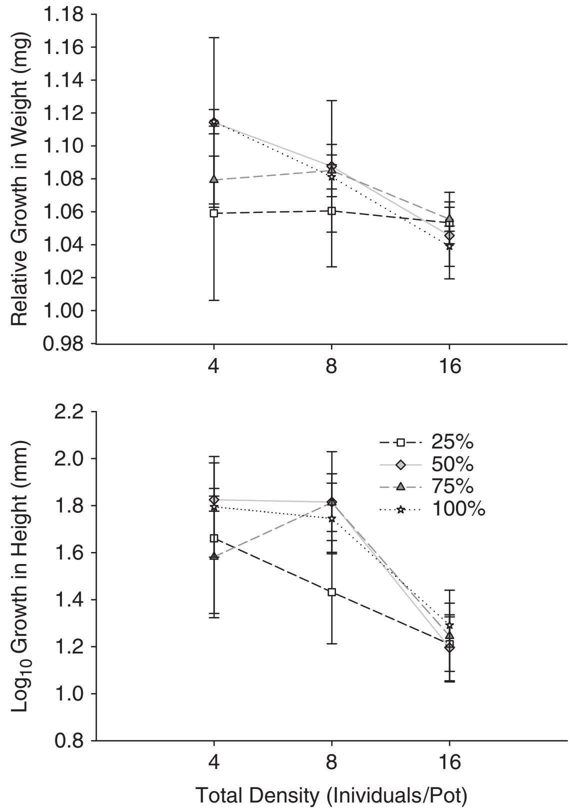

Fig. 3. Relative growth in height and biomass of *Ambrosia* in the greenhouse response surface experiments. Three total densities of both species were combined in five relative abundances of *Ambrosia* seedlings for a total of 15 treatment combinations. Each combination was replicated four times.

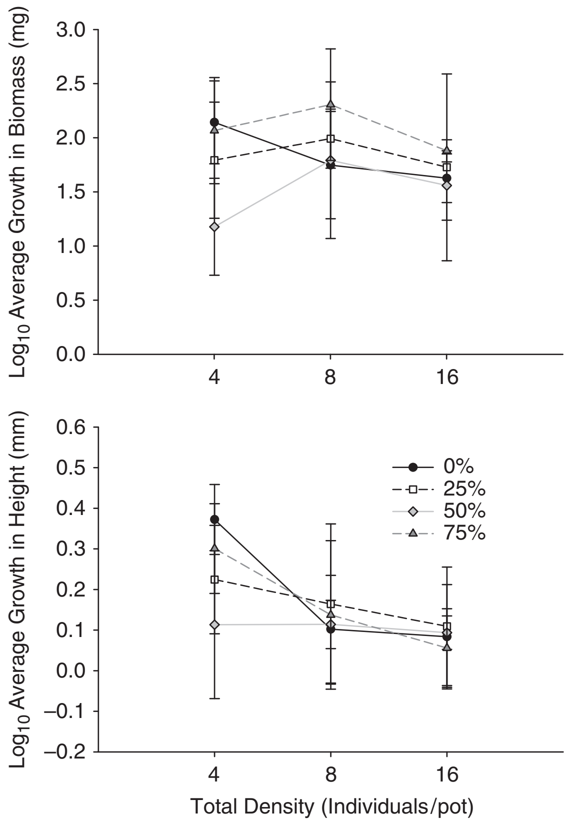

Fig. 4. Relative growth in height and biomass of *Schismus* in the greenhouse response surface experiments. Three total densities of both species were combined in five relative abundances of *Ambrosia* seedlings for a total of 15 treatment combinations. Each combination was replicated four times.

$P = 0.188$). Thus, at higher densities, plants produced smaller seeds.

Discussion

Facilitated establishment of annuals and perennials is an important dynamic of arid plant communities. These dynamics are potentially damaging to system integrity when harmful, invasive species are facilitated by native plants. Spatial variability in natural plant populations is the result of factors acting at different scales. By using a combination of observational and manipulative studies, we identified relevant patterns and tested mechanisms that may produce the observed patterns. Our field survey, which identified the spatial signature of interactions occurring without manipulation, showed that *Ambrosia* and *Schismus* respond to the small-scale heterogeneity defined by well-established shrubs, and that neither species is segregated in space. Moreover, our field manipulations showed that *Ambrosia* adults enhance *Schismus* individual growth. Because *Ambrosia* seedlings are most commonly found under conspecific canopies (Miriti et al. 1998; Schenk et al. 2003), competition between *Schismus* and *Ambrosia* seedlings is a critical dynamic that likely influences population growth and spatial distribution of both species. Our greenhouse results contextualized competition between *Ambrosia* and *Schismus* seedlings, showing that high densities of *Schismus* reduce growth of *Ambrosia* seedlings. Because *Ambrosia* is an important nurse plant to a variety of annuals and perennials in this and other regions, unmanaged *Schismus* invasion may, in the long term, cause reductions in the diversity of annuals and perennials within our study system.

Spatial distribution of Schismus

The spatial variability of *Schismus* densities in natural populations is the result of factors acting at different scales. The small-scale (at distances <3 m) positive autocorrelation in *Schismus* abundance reflects short- and long-term microhabitat differences induced by shrubs, such as variation in seed deposition (Reichman 1984; De Soyza et al. 1997; Guo et al. 1998) and germination rates (Pugnaire & Lázaro 2000) among microhabitats, or small-scale changes in soil properties (Schlesinger & Pilmanis 1998; Perry et al. 2002). Positive autocorrelations at larger scales suggest that *Schismus* may be responding to processes acting at scales larger than the individual shrub spatial domain. These processes, such as geomorphological changes in soil properties, generate patterns that vary at regional scales (e.g., Perry et al. 2002; Rosenberg 2004) and are beyond the scope of our study. To be conservative, we have limited our interpretations to local interactions between our focal species.

Interactions between Schismus and Ambrosia

Our results indicate a net positive effect of *Ambrosia* on *Schismus* when growth under *Ambrosia* canopies was compared to that in open areas. Several documented factors may contribute to this net facilitation. Annual species show higher biomass and seed production below *Ambrosia* canopies (Tielbörger & Kadmon 1995; Holzapfel & Mahall 1999). Reduced root competition is one mechanism that has been shown to improve *Schismus* performance under *Ambrosia* canopies (Holzapfel & Mahall 1999). Because superficial root distribution around *Ambrosia* decreases at distances beyond 1 m from the center of shrubs (Hartle et al. 2006), *Schismus* plants growing in open areas typically do not experience intense root competition. We cannot address root effects in the field because our use of PVC pipes equalizes superficial root effects across treatments. In light of empirical studies in similar systems, our results suggest that plants growing far from *Ambrosia* adults may be compromised by poor soil conditions and high light intensities.

Interestingly, our results suggest that individual *Schismus* biomass is not very sensitive to small-scale changes in soil properties or highly responsive to high intraspecific density. It is expected that as soil nutrient content decreases with distance from *Ambrosia* shrubs (Schlesinger & Pilmanis 1998; Titus et al. 2002), competition for resources increases. This relationship between resources and competition should have produced shorter individuals far from *Ambrosia* plants and a significant effect of the biomass of competitors. Although we detected a reduction in biomass with distance, this trend, as well as the effect of competitors, was not significant. In addition, *Schismus* showed high tolerance to density of conspecifics. In our field experimental populations, we detected negative effects of density on individual growth, with densities $>3000/m^2$, which greatly exceeds average densities in natural population (1200 individual m^{-2} in our study and 214 seedlings m^{-2} in a 24 year study – Venable 2007). In fact, we did not detect a significant effect of density on *Schismus* individual growth in our greenhouse experiment, in which we used a range of densities that are commonly found in natural populations.

Finally, our results revealed that areas close to shrubs do not favor germination. We recorded higher germination in open areas after seed addition, which implies that lower densities in intershrub areas detected in natural populations reflect dispersal limitation and not less favorable germination conditions. Thus, our results suggest that the net positive effect of *Ambrosia* on *Schismus* populations is controlled by secondary dispersal, which tends to accumulate seeds below canopies (Reichman 1984; De Soyza et al. 1997; Guo et al. 1998), and higher germination probabilities in open areas.

Effect of Schismus over Ambrosia seedlings

Densities of *Schismus* can vary up to three orders of magnitude (0–1621 seedlings m^{-2}, mean = 214.2, SD = 346.4 seedlings m^{-2} in a 24-year study – Venable 2007) in natural populations. Inter-annual variations in temperature and precipitation influence both seed set and germination of dispersed seeds (Pake & Venable 1995; Chesson et al. 2004). The seed densities used in our greenhouse experiment are in the range of these naturally occurring densities, and results from this experiment suggest *Schismus* seed densities negatively impact growth rates of *Ambrosia* seedlings. Biomass and reproductive effort of *Schismus* were favored at intermediate total densities, but *Ambrosia* decreased in growth and biomass with increasing densities of both species. Furthermore, equivalent effects of competition were detected along the replacement series for *Ambrosia*, but not for *Schismus*. Because *Ambrosia* seedlings are frequently found close to parent plants (Guo et al. 1998; Miriti et al. 2001; Housman et al. 2003; Schenk et al. 2003), our observed high densities of *Schismus* under *Ambrosia* canopies may decrease recruitment of *Ambrosia* seedlings in years that present high germination for annuals in general, or high densities of *Schismus* in particular.

In conclusion, we found that presence of *Ambrosia* strongly influenced performance of individual *Schismus*, although in natural populations other ecosystem processes may mediate this response. *Schismus* germination is favored far from *Ambrosia*, while individual performance is favored close to perennials. Interspecific competition may compromise *Ambrosia* seedling survival when *Schismus* is of sufficiently high density, which, in turn, could strongly reduce the overall recruitment of *Ambrosia*. Ultimately, interactions between *Ambrosia* and *Schismus* may strongly influence long-term population dynamics of both species.

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