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Positive and negative plant interactions contribute to a north-south-patterned association between two desert shrub species

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Abstract Abiotic factors are often thought to be the predominant forces shaping desert plant communities. But both positive and negative interactions between plants are frequently observed in deserts, and it is an open question whether they can strongly affect the spatial structure of a desert community. The goal of this study was to answer this question for a plant community in the North American Mojave Desert. Two semi-shrub species, *Ambrosia dumosa* and *Acamptopappus sphaerocephalus*, were the focus of this study. At the study site, seedlings emerged predominantly on the northern side of shrubs, indicating positive effects of canopy shading on emergence, but survival of *Ambrosia* seedlings was much higher in open areas than at the edge of conspecific shrubs. Negative intraspecific interactions also affected *Ambrosia* shrubs, which did not increase in size over a 4-year period unless the nearest conspecific neighbor had been removed. These negative intraspecific interactions among different life stages of *Ambrosia* appear to contribute to spatial segregation observed among shrubs of this species. In contrast, *Acamptopappus* shrubs and their seedlings were aggregated with *Ambrosia* shrubs, and occurred more often on the northern side of *Ambrosia* than expected by chance. Removal of *Ambrosia* neighbors positively affected growth of *Acamptopappus*, but only when the neighbor was removed on the northern side. For *Acamptopappus*, an *Ambrosia* neighbor on the southern side may have some positive effects, which appear to neutralize the negative effects found for northern neighbors. These positive effects were likely at least

partly due to shading. Removal of *Ambrosia* neighbors negatively affected predawn xylem pressure potentials of *Acamptopappus*, but this effect was only found during one growing season and was briefly reversed during the next. In summary, negative intraspecific interactions appear to cause spatial segregation of *Ambrosia* shrubs, while a combination of positive and negative interactions apparently contribute to the directional association between *Ambrosia* and *Acamptopappus*. Thus plant interactions in this desert appear to shape community structure in at least two dimensions by influencing the distances and in which directions to their neighbors plants can grow and survive.

Keywords Competition · Facilitation · Seedling survival · Directionality · Spatial patterns

Introduction

A recent meta-analysis of studies on plant interactions found that ecosystems of low productivity, such as deserts, are the ones most likely to have intense competitive and facilitative interactions between plants (Goldberg et al. 1999). Other findings also suggest that both positive and negative plant interactions are common and often concurrent in desert plant communities (e.g., Casper 1996; Holzapfel and Mahall 1999; Tielbörger and Kadmon 2000), which poses the question whether such interactions are important for shaping the structure and function of these communities. Interactions between neighboring plants may fail to strongly affect plant growth and survival if they are unimportant relative to other factors, such as the harsh and variable desert climate, soil heterogeneity, microtopography, disturbances, pathogens, or herbivory (Grime 1973; Welden and Slauson 1986). Thus, the question is not only whether plant interactions are intense in any given system (Goldberg et al. 1999), but also whether they actually matter for shaping community structure (Ehleringer 1984; Fonteyn and Mahall 1978, 1981).

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Here we attempt to answer this question for a plant community in the Mojave Desert of North America, focusing on two drought-deciduous semi-shrub species, *Ambrosia dumosa* (A. Gray) Payne and *Acamptopappus sphaerocephalus* (A. Gray) A. Gray (both Asteraceae). These species contribute about 60% of the biomass in this community, with shrubs of *Larrea tridentata* (DC.) Cov. (26%) and winter annuals (13%) contributing most of the rest (Schenk 1998). Spatial patterns of shrubs and shrub seedlings in this community were analyzed, and studies of plant interactions were conducted to determine whether the observed spatial pattern in the locations and sizes of individual plants relative to their neighbors corresponded with positive and negative plant interactions between neighboring plants.

To formulate hypotheses about plant interactions, we compared spatial patterns between life stages and species. Comparisons of spatial patterns in seedlings and mature plants were done because they can suggest how the patterns in the mature plants may have developed (Callaway 1998; Chapin et al. 1989; Moeur 1997). Comparative analyses of patterns among and within coexisting species can suggest differences between intra- and interspecific interactions (e.g., Fonteyn and Mahall 1981; Haase et al. 1996). We also took the directionality of spatial patterns into account, because desert plants on the more shaded northern side of neighbors may be positively (Valiente-Banuet et al. 1991) or negatively affected by the shade (Forseth et al. 2001).

Spatial patterns at the study site were analyzed by Schenk (1998) and are summarized in Fig. 1. Seedlings of both species emerged 10–20 times more frequently on the northern side of semi-shrubs than on their southern side. Microsites of seedling emergence at the northern canopy edge of semi-shrubs were shaded for at least parts of the day and had on average significantly lower soil surface temperatures than microsites at the southern edge of shrubs or in open areas (Schenk 1998), which suggests that seedling emergence was facilitated by canopy shade. In contrast to seedlings, which were strongly and directionally aggregated with conspecific shrubs, mature shrubs of both species were intraspecifically segregated. *Acamptopappus* shrubs occurred more frequently than expected from a random pattern on the northern side of mature *Ambrosia* shrubs, partly mirroring the distribution of its seedlings. Mature plants of these two species therefore were directionally aggregated with each other.

Our observations of spatial patterns led us to the following hypotheses: (1) seedlings are more likely to survive when growing at a distance from conspecific shrubs; (2) effects of *Acamptopappus* shrubs on the survival of *Ambrosia* seedlings are less negative than those of *Ambrosia* shrubs on conspecific seedlings; (3) intraspecific interactions between mature shrubs are predominantly negative; and (4) mature *Acamptopappus* shrubs are less negatively affected by an *Ambrosia* neighbor on their southern side than by one on their northern side. To test these hypotheses, we measured survival and perfor-

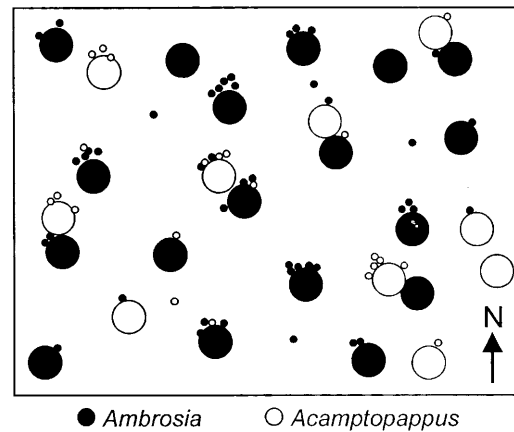


Fig. 1 Schematic of the main spatial patterns found between *Ambrosia dumosa* and *Acamptopappus sphaerocephalus* at the study site (after Schenk 1998). Large circles symbolize mature shrubs and small circles symbolize seedlings during the first months after emergence. The following patterns are illustrated: (1) About 95% of all seedlings of both species emerged within 20 cm of the canopy edge of a semi-shrub of either species, and they emerged 10–20 times more frequently on the more shaded northern side of soil mounds associated with semi-shrubs than on their southern side. (2) Intraspecific segregation (i.e., regular distribution) of mature shrubs was observed in both species. (3) Mature *Acamptopappus* shrubs occurred frequently (~1.5 times more than expected in a random pattern) on the northern to northwestern side of mature *Ambrosia* shrubs

mance of *Ambrosia* seedlings in the field and in the greenhouse and conducted nearest neighbor removals of mature shrubs in order to measure effects of neighbors on the water status and growth of the shrubs.

Materials and methods

Study site

The study site was located in northeastern Fremont Valley, California, at the western edge of the Mojave Desert (35°23' N, 117°41' W) at 804 m elevation. The climate is arid, with most precipitation falling in winter and spring. Mean annual precipitation is about 130 mm. The study spanned four growing seasons (September to August) that varied greatly in precipitation (1996/1997: 83 mm; 1997/1998: 338 mm; 1998/1999: 95 mm; 1999/2000: 96 mm). The soil consists of aeolian sand deposits, forming a 0.6 to >1.1 m deep surface layer of torripsamments (Soil Survey Staff 1998) with generally low percentages of gravel over deeper layers of gravelly, loamy sand. Clay contents of the soil are about 1.5%, and silt contents are about 8.5% (Schenk 1998). At the site, small mounds of soil accumulate at the base of each shrub, and the shrub mounds tend to be more fertile than the nutrient-poor shrub interspaces, probably due to litter input, concentration of animal activities at shrub mounds, and erosion between mounds (Charley and West 1975; Schlesinger et al. 1996; Wallace and Romney 1980).

The vegetation is Mojave creosote-bush scrub (Vasek and Barbour 1977), co-dominated by the evergreen shrub *Larrea tridentata* and the drought-deciduous semi-shrubs *Ambrosia dumosa* and *Acamptopappus sphaerocephalus* var. *hirtellus*. Plant nomenclature follows Hickman (1993). The phenology of the drought-deciduous species depends strongly on the timing of major rainfall events, which typically occur between fall and early spring. Both species are multi-stemmed at ground level, with stems splitting into separate parts once the shrubs reach diameters of above 50 cm

(Schenk 1999). The semi-shrubs fill the large interspaces between *Larrea* shrubs and are spatially segregated from *Larrea*. The area was occasionally grazed by sheep in the past, but has been protected from grazing since at least 1989.

Seedling experiments in the field

To determine the effects of the proximity of shrubs on the survival and performance of *Ambrosia* seedlings, mortality, heights and numbers of green leaves of naturally established, marked *Ambrosia* seedlings were repeatedly measured from October 1997 to August 1998, and again in May 1999. Seedlings were randomly chosen and were marked at the beginning of October 1997, a few days after emergence. Of 120 marked seedlings, 50 were on northern slopes of 20 *Ambrosia* shrub-mounds, 50 were on northern slopes of 20 *Acamptopappus* shrub-mounds, and 20 were in open areas between shrubs.

Seedling survival was analyzed using SYSTAT (Steinberg et al. 1998) by calculating Kaplan-Meier estimates of survival curves for the three locations, followed by a Mantel-Cox test. Pointwise 95% confidence intervals for the estimated survival probabilities were calculated by the linear, normal approximation method of Thomas and Grunkemeier (1975). As an indicator of seedling performance we calculated "leaf-days" for each seedling by multiplying the number of true, green leaves measured at the end of a given time interval by the number of days in the interval, using linear interpolations of leaf numbers between dates, and summing these leaf \times days estimates over the whole growing season (265 days from 1 October 1997). The data were square-root transformed to normalize the distributions and analyzed by one-way ANOVA followed by a Scheffé-test. Measurements of seedling heights were analyzed by repeated measures ANOVA using SYSTAT MGLH (Wilkinson 1990), followed by a Scheffé-test.

Seedling experiment in the greenhouse

This experiment was conducted to determine whether seedlings were affected by differences in soil characteristics among three microsites, the northern edge (± 10 cm) of canopies of *Ambrosia* or *Acamptopappus* shrubs [predominant locations of natural seedling emergence (Schenk 1998)] and open areas between shrubs. Soil was taken in August 1997 from the top 5 cm of the profile. The soil was air-dried, mixed to one field-composite sample for each microsite, and sieved through a 7 mm sieve to remove coarse litter and large stones. Contents of organic carbon and total nitrogen in the soil were determined using a Carlo Erba CN analyzer (model NA 1500 NC). For these analyses, samples were oven-dried at 70°C and sieved through a 2 mm soil-sieve to remove gravel and large organic material. Carbonates were removed from the soil by the HCl vapor acidification method of Hedges and Stern (1984) prior to the determination of organic carbon content.

We were unable to germinate enough *Acamptopappus* seeds for growth experiments, and therefore used *Ambrosia* seedlings only. *Ambrosia* diaspores (1-seeded burs), were collected in spring 1997 from the study site and were germinated in wet, sterile sand. As soon as the radicles emerged, one fruit was transplanted into each of 60, 9 \times 9 \times 7 cm pots. The bottom holes of the pots were covered with Nitex nylon cloth (Tetko, Briarcliff Manor, N.Y., USA) with 25- μ m openings to restrict root growth but allow water flow. Twenty replicate pots for each of the three soil treatments were arranged randomly in the greenhouse for the 4-week duration of the experiment. They were watered to field capacity once a week to avoid effects of water limitation on seedling growth and were weeded throughout the experiment to eliminate competition.

After 4 weeks, seedlings were harvested by submerging the pots in water and gently removing the plants from the soil to avoid damage to the root systems. Remaining soil particles adhering to the roots were removed with tweezers. Plants were separated into shoots and roots. Seedlings with aborted primary roots were excluded from the analyses, as previous studies had shown that this

was most likely caused by damage during transplantation. This reduced the number of replicates to 14 with shrub-interspace soil, 17 with *Ambrosia* soil, and 14 with *Acamptopappus* soil. Root length was measured with a digital image analysis system (model DIAS II, Decagon Devices, Pullman, Wash.), using a method slightly modified from that described in Harris and Campbell (1989). After measurements, shoots and roots were oven-dried at 70°C and weighed separately.

Shrub removal experiments

The presence of interactions between mature shrubs was tested in the field using a nearest-neighbor removal design. Forty-five nearest-neighbor pairs of *Ambrosia* and *Acamptopappus*, as well as 30 conspecific pairs of *Ambrosia*, were chosen in a 60 \times 70 m area, and nearest neighbor removal treatments were randomly assigned. Mean shrub sizes were similar for both species (*Ambrosia*: 73 \pm 2 cm diameter; *Acamptopappus*: 70 \pm 2 cm), but the mean distance between interspecific neighbors was shorter (47 \pm 2 cm from center to center) than distances between conspecific *Ambrosia* neighbors (75 \pm 4 cm). Three combinations of nearest neighbors were included in these experiments: *Ambrosia* with *Acamptopappus* as nearest neighbor; *Ambrosia* with *Ambrosia* as nearest neighbor; and *Acamptopappus* with *Ambrosia* as nearest neighbor. Conspecific neighbor pairs of *Acamptopappus* were too rare on the site to allow removal experiments. In 15 randomly selected pairs of each of these three combinations the nearest neighbor was removed. The remaining pairs served as controls. Removals were done by cutting shrubs at ground level in February 1997 before leaf emergence. Re-growth was only observed in *Ambrosia* and was removed throughout the course of the experiments.

All shrubs were mapped using a total station transit (model GTS-3B, Topcon, Paramus, N.J., USA). Two canopy diameters, representing the maximum extent of the living canopy in the north-south and east-west direction, were measured before the beginning of the experiment in November 1996 and again in November 2000. Size measurements were used to calculate above-ground biomass estimates, based on measurements of harvested shrubs (Schenk 1998). Size changes were expressed as relative above-ground growth (aboveground biomass at beginning of experiment / aboveground biomass at end of experiment).

Measurements of predawn xylem pressure potential (Ψ) began after leaf emergence during two growing seasons, in spring 1997 and late summer 1997 to winter 1997/98, using a pressure chamber (PMS Instruments, Corvallis, Ore., USA). To measure Ψ , one terminal twig with green leaves or buds was cut from each shrub before dawn, immediately placed in a small plastic bag, and measured within 40 min of being cut. Pilot studies had shown that storage of up to an hour at cool night-time temperatures did not affect measurements of Ψ , which were consistently below -1 MPa.

For statistical analyses, Ψ data were multiplied by -1 and log-transformed. The overall effects of treatments on pressure potentials were analyzed by repeated measures analyses of covariance (Potvin et al. 1990) using SYSTAT (Wilkinson 1990). To account for potential violations of the equality of covariances assumption, within-subject effects with more than one degree of freedom in the numerator were considered significant at the $P < 0.05$ level when both the Huynh-Feldt and Greenhouse-Geisser adjusted P -values were < 0.05 . The ANOVAs were followed by planned contrast comparisons to analyze differences between treatments and controls for each measuring date. Relative growth data were analyzed in ANOVAs using SYSTAT (Wilkinson 1990) with treatment (removal versus control), species, and direction to the nearest neighbor (north $\pm 90^\circ$ or south $\pm 90^\circ$) as categorical variables.

Because soil water availability and plant growth rates may vary spatially over an area of 60 \times 70 m size, we performed trend surface analyses (Bailey and Gatrell 1995) by regressing Ψ and growth data against the X, Y, and Z (elevation) coordinates of the shrubs. Where spatial trends were detected, spatial coordinates, or their linearizing transformations, were included as covariates in the ANCOVAs. We also tested for possible effects of additional

factors on the performance of shrubs by regressing Ψ and growth data against shrub biomass, nearest-neighbor biomass, and distance to the nearest neighbor. None of these regressions were significant, and these factors were therefore not included in the ANCOVAs.

Results

Seedling experiments in the field

Survival of *Ambrosia* seedlings that had germinated within a few days of 1 October 1997 was above 90% until mid-January 1998 (109 days after germination). During this period, survival did not differ between *Ambrosia* seedlings that had germinated in open areas, at the edge of *Ambrosia*, or at the edge of *Acamptopappus* shrubs. Survival remained above 90% for seedlings growing in open areas until the end of the growing season (June 1998), but seedlings at the edge of shrubs experienced significantly higher mortality during the later part of the growing season (Fig. 2A). By the end of the growing season, 265 days after germination, only 22% of the seedlings growing at the edge of *Ambrosia* were still alive, compared to 48% at the edge of *Acamptopappus* and 95% in open areas, with survival in all three locations being significantly different from each other ($P < 0.05$). Survival during the dry season could not be monitored because dead seedlings could not be distinguished with any certainty from live ones that had dropped their leaves. At the end of the second growing season (31 May 1999, 608 days after germination), only 2% of the seedlings growing at the edge of *Ambrosia* were still alive, compared to 10% at the edge of *Acamptopappus* and 42% in open areas. Visual inspections indicated that herbivory or pathogens were not responsible for most of the seedling mortality. The observations support our hypothesis (1) that seedlings are more likely to survive when growing at a distance from conspecific shrubs, and also support hypothesis (2) that effects of *Acamptopappus* shrubs on the survival of *Ambrosia* seedlings are less negative than those of *Ambrosia* shrubs on conspecific seedlings.

Ambrosia seedlings in open areas had more leaves than those growing close to either shrub species from 30 days after germination to the end of the first growing season (Fig. 2B). The leaf \times days analysis showed a significantly ($P < 0.001$) higher potential for carbon gain for seedlings growing in open areas ($2,508 \pm 182$ leaf \times days) than for those at the edge of shrubs (edge of *Ambrosia*: 804 ± 115 ; edge of *Acamptopappus*: 982 ± 115), with no significant differences between seedlings growing at the edge of the two shrub species. Moreover, visual inspection showed that leaves of seedlings in open areas tended to be larger than those of seedlings under shrubs. Seedling heights did not differ among the three locations (Fig. 2C; ANOVA: Sum-of-squares 43.1, $df=2$, $F=1.56$, $P > 0.05$), but the few seedlings that survived to the end of the growing season at the edge of *Ambrosia* shrubs tended to be taller than those in the other two locations (Fig. 2C).

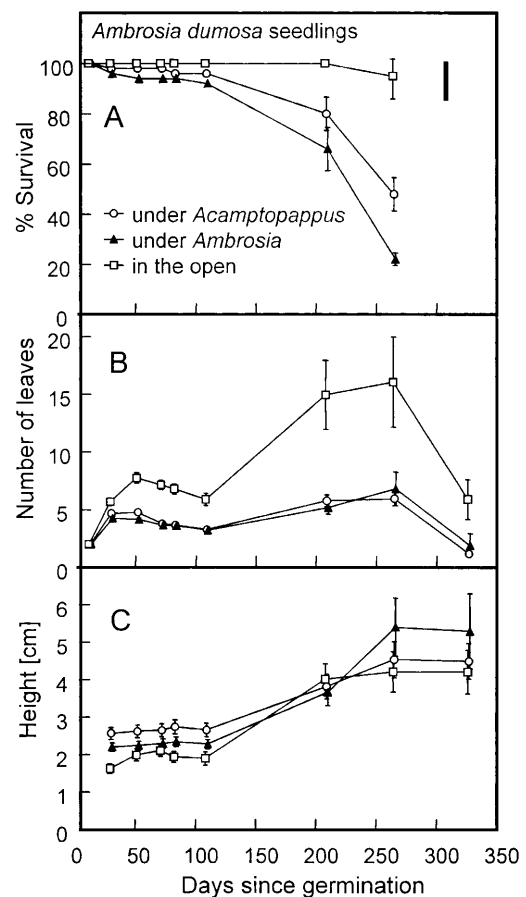


Fig. 2A–C First-season survival and performance of *Ambrosia dumosa* seedlings that had germinated on approximately 1 October 1997. The error bars in **A** depict the 95% confidence intervals for the Kaplan-Meier estimates of the survival curves. Confidence intervals for the survival curves between 0 and 150 days after germination overlapped substantially for seedlings growing in the three locations, and survival percentages within the range of the black bar on the upper, right-hand side of the graph were not significantly different from each other. **B** and **C** show the numbers of leaves (excluding cotyledons) and heights of surviving seedlings, respectively. Error bars in **B** and **C** are ± 1 SE

Greenhouse seedling experiments

Ambrosia seedlings grown in soil from shrub interspaces were similar in shoot-, root-, and total biomass to those grown in soil from the slopes of *Ambrosia* mounds (Table 1). Seedlings from either of these treatments were, on average, about twice as large as seedlings grown in soil from the slopes of *Acamptopappus* mounds (Table 1), suggesting that the soil from *Acamptopappus* mounds may have contained inhibiting substances or pathogens. The mean total root length of seedlings grown in soil from open areas or in soil from *Ambrosia* mounds was about twice that of seedlings growing in soil from *Acamptopappus* mounds ($P < 0.05$). The different soils did not have significant effects on the numbers of leaves per plant at harvest or on root/shoot ratios.

Total organic carbon content in soil from shrub mounds was about twice as high as in soil from open ar-

Table 1 Sizes of *Ambrosia dumosa* seedlings after 28 days of growth in surface soil (0–5 cm) taken from the northern edge of *Ambrosia*-mounds, *Acamptopappus sphaerocephalus*-mounds, and from open areas between shrubs. Differences between seedlings

| Soil: | Shrub interspace | <i>Ambrosia</i> mounds | <i>Acamptopappus</i> mounds |
|--------------------------|-------------------------|-------------------------|-----------------------------|
| Root biomass (mg) | 8.9 ^a ±1.0 | 7.5 ^a ±1.0 | 3.9 ^b ±0.6 |
| Root length (m) | 1.32 ^a ±0.19 | 1.19 ^a ±0.17 | 0.64 ^b ±0.09 |
| Shoot biomass (mg) | 23.5 ^a ±2.9 | 20.8 ^{ab} ±2.7 | 12.6 ^b ±1.9 |
| Total biomass (mg) | 32.4 ^a ±3.9 | 28.3 ^a ±3.6 | 16.5 ^b ±2.4 |
| Number of leaves | 8.6 ^a ±0.4 | 8.2 ^a ±0.4 | 7.4 ^a ±0.5 |
| Root/shoot ratio (mg/mg) | 0.39 ^a ±0.02 | 0.38 ^a ±0.05 | 0.32 ^a ±0.03 |

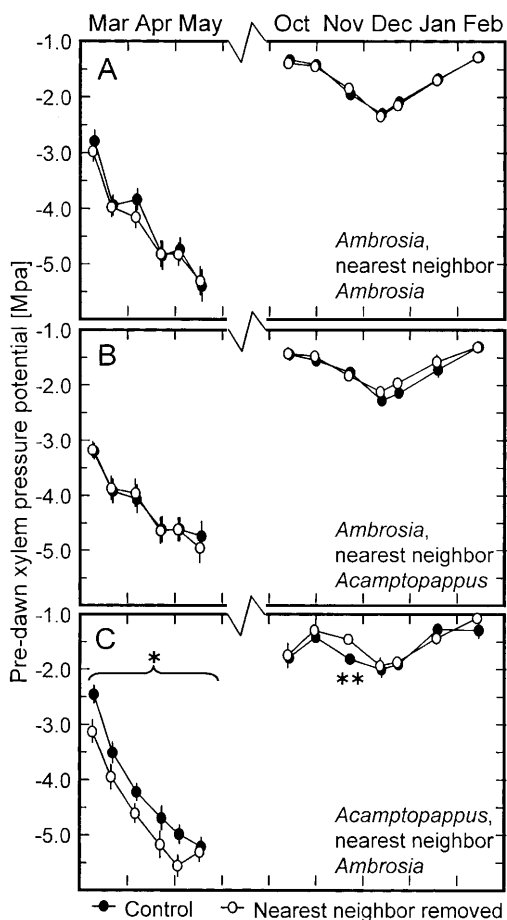


Fig. 3 Pre-dawn xylem pressure potentials (\pm SE) of *Ambrosia dumosa* and *Acamptopappus sphaerocephalus* shrubs for different combinations of neighbors, measured during spring 1997 and during fall 1997 to winter 1997/98. For removal treatments, nearest neighbors were removed in February 1997. Removal treatments were significantly different over the period indicated by an asterisk (repeated measures ANCOVA: Sum-of-squares = 0.061; $df=1$; F -ratio = 5.01; $P=0.035$), and significantly different from controls on the date indicated by two asterisks (planned contrast comparison; $P<0.01$)

eas ($n=5$, $P<0.05$), but total organic carbon content of soil from shrub mounds of the two species was similar (contents in g kg^{-1} dry soil: open areas 0.77 ± 0.02 ; *Ambrosia* mounds 1.55 ± 0.14 ; *Acamptopappus* mounds

grown in different soil types were analyzed by one-way ANOVAs, using SYSTAT MGLH (Wilkinson 1990). Significantly different values ($P<0.05$) within the same row are indicated by different superscripts

1.60 ± 0.31). Total nitrogen contents were about 50% higher in shrub-mound soil than in soil from open areas ($n=5$, $P<0.05$), but there were no significant differences between mounds of the species in total soil nitrogen contents (values in g kg^{-1} dry soil: open areas 0.12 ± 0.01 ; *Ambrosia* shrub mounds 0.16 ± 0.01 ; *Acamptopappus* mounds 0.19 ± 0.02).

Shrub removal experiments

Shrubs leafed out in late February 1997 in response to winter rains. During the following drying cycle, Ψ s of *Ambrosia* shrubs showed no effects of nearest neighbor removal, regardless of neighbor species (Fig. 3 A, B). In contrast, *Acamptopappus* shrubs with *Ambrosia* neighbors removed had more negative Ψ s than the controls (Fig. 3C), suggesting that the water status of the controls was positively affected by the presence of *Ambrosia* neighbors. These effects were found when accounting for significant ($P<0.01$) spatial trends of Ψ s in the experimental plot, with Ψ s on average decreasing slightly from the southern to the northern edge of the experimental plot.

After rains in late September 1997, *Ambrosia* shrubs leafed out in early October, while *Acamptopappus* shrubs leafed out more slowly. In the latter half of November, *Acamptopappus* shrubs with *Ambrosia* neighbors present developed lower Ψ s than those in the removal treatments (Fig. 3C; $P<0.01$). After a series of rains, effects of removal treatments were no longer discernible from December on. *Ambrosia* shrubs showed no effects of neighbor removal (of either species) on Ψ s through fall and winter 1997/98 (Fig. 3 A, B). Spatial trends of Ψ s in the experimental plots during this period were not statistically significant (data not shown).

Mean biomass of *Ambrosia* shrubs in the presence of *Ambrosia* neighbors did not increase over the 4-year study period, while mean biomass of *Ambrosia* shrubs in the absence of conspecific neighbors increased by about 19% ($P<0.05$; Table 2). These results support hypothesis (3) that intraspecific interactions between mature *Ambrosia* shrubs were predominantly negative. Mean biomass of *Ambrosia* shrubs with or without *Acamptopappus* neighbors increased by 14% and 25%, respectively, with

Table 2 Performance measures (± 1 SE) of *Ambrosia dumosa* and *Acamptopappus sphaerocephalus* shrubs in nearest-neighbor removal experiments. Estimates of biomass increases and relative aboveground growth (RAG) were calculated from canopy-size measurements on 17 November 2000, relative to measurements from 13 November 1996 ($n=15$). Statistical analyses were done by

| Species: | <i>Ambrosia</i> | | | | <i>Acamptopappus</i> | |
|----------------------|------------------|------------------|----------------------|------------------|----------------------|------------------|
| Neighbor: | <i>Ambrosia</i> | | <i>Acamptopappus</i> | | <i>Ambrosia</i> | |
| Treatment: | Neighbor present | Neighbor removed | Neighbor present | Neighbor removed | Neighbor present | Neighbor removed |
| Biomass increase (g) | 0 \pm 31 | 103** \pm 28 | 78 \pm 26 | 104 \pm 24 | -70 \pm 93 | -18 \pm 65 |
| RAG (kg/kg) | 0.00 \pm 0.05 | 0.19* \pm 0.05 | 0.14 \pm 0.04 | 0.25 \pm 0.06 | -0.21 \pm 0.11 | -0.04 \pm 0.14 |

Table 3 Three-way ANOVA ($n=60$; $r^2=0.4061$) of the effects of allospecific neighbor removal on aboveground relative growth over the 4-year study period. Estimates of relative aboveground growth (in grams) were calculated from canopy-size measurements on 17 November 2000, relative to measurements from 13 November 1996. Included as categorical variables were neighbor removal versus control, species measured (*Ambrosia dumosa* or *Acamptopappus sphaerocephalus*), and direction to the nearest neighbor ($N\pm 90^\circ$ or $S\pm 90^\circ$), with log-transformed Y -coordinates as covariates to account for spatial trends. Shown are sums of squares (SS), degrees of freedom (df), F -ratios (F), P -values (P)

| Source | SS | df | F | P |
|---|-----------|------|-------|-------|
| Removal | 593,943 | 1 | 5.27 | 0.026 |
| Species | 1,311,990 | 1 | 11.65 | 0.001 |
| Direction | 195,631 | 1 | 1.74 | 0.193 |
| Removal \times species | 90,217 | 1 | 0.80 | 0.375 |
| Removal \times direction | 692,923 | 1 | 6.15 | 0.016 |
| Species \times direction | 2,497 | 1 | 0.02 | 0.882 |
| Removal \times species \times direction | 508,226 | 1 | 4.51 | 0.039 |
| Spatial trend | 960,145 | 1 | 8.53 | 0.005 |
| Error | 5,743,950 | 51 | | |

no significant differences between treatments (Table 2). Relative growth of *Ambrosia* in the presence of *Ambrosia* neighbors was lower than that of *Ambrosia* in the presence of *Acamptopappus* neighbors ($P<0.05$). *Acamptopappus* biomass decreased over the 4-year study period by about 12% (Table 2).

Effects of *Ambrosia* neighbor removals on growth of *Acamptopappus* were statistically significant ($P<0.05$; Table 3) when the direction to the neighbor was taken into account. All *Acamptopappus* shrubs that had had *Ambrosia* neighbors removed on the northern side increased in biomass, while all those with an *Ambrosia* neighbor present on their northern side decreased in biomass (Fig. 4). *Acamptopappus* shrubs with neighbors present or absent on the southern side mostly decreased in biomass, and there was no significant difference between removal and control. The observation that neighbor removal on the northern side had a strong positive effect on *Acamptopappus* growth, while neighbor removal on the southern side had no effect supported our hypothesis (4) that mature *Acamptopappus* shrubs are less negative-

ANOVA and tests between treatments and controls were conducted as planned contrasts between removal treatments and appropriate controls. Measures that differed significantly in the removal treatment from the controls are indicated by * ($P<0.05$) or ** ($P<0.01$)

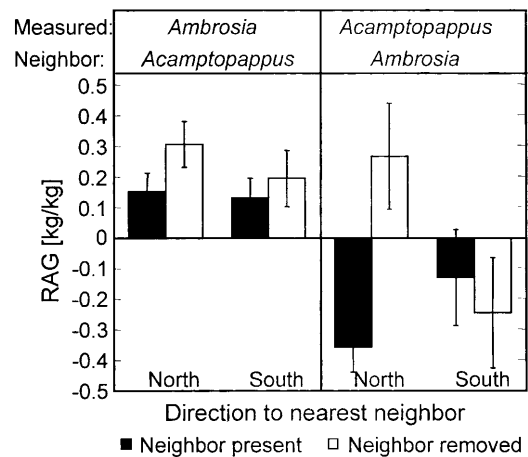


Fig. 4 Effects of removal of nearest, allospecific shrub neighbors on estimates of relative aboveground growth (RAG ± 1 SE) for the period from November 1996 to November 2000. Shown are data for *Ambrosia dumosa* shrubs with *Acamptopappus sphaerocephalus* shrubs as nearest neighbors (left) and for *Acamptopappus* shrubs with *Ambrosia* shrubs as nearest neighbors (right). Statistical analyses of these data are presented in Table 3

ly affected by having an *Ambrosia* neighbor on their southern side than by having one on their northern side.

Discussion

The results of this study supported all four of our hypotheses about positive and negative plant interactions that had been based on observations of spatial patterns in shrubs and shrub seedlings.

Seedling survival and performance

Ambrosia seedlings grew better and were more likely to survive when growing at a distance from conspecific mature shrubs (Fig. 2), and this observation is in agreement with similar findings in other studies (Hunter 1989; Miriti et al. 1998; Prose et al. 1987; Vasek 1979/80; Walker

et al. 2001). The negative effects of *Ambrosia* shrubs on conspecific seedlings may have been caused by a combination of shading (Walker et al. 2001), competition with annuals that tend to be associated with *Ambrosia* shrubs (Holzapfel and Mahall 1999; Muller 1953), and interactions with roots of conspecific shrubs and seedlings (Miriti et al. 1998). Previous studies have found that root growth of *Ambrosia* is inhibited by contact with roots from other *Ambrosia* individuals (Mahall and Callaway 1991, 1992, 1996). This may be viewed as the defense of a root territory by shrubs (Schenk et al. 1999), and could be a potent means of inhibiting growth of *Ambrosia* seedlings where soil is densely occupied by *Ambrosia* shrub roots.

Ambrosia seedlings apparently were not affected by differences in the soil between microsites, which makes it unlikely that allelochemicals or soil pathogens contributed to the negative effects of shrubs on seedlings. Surprisingly, seedlings in the greenhouse experiments did not grow better in the more fertile soil from *Ambrosia* shrub mounds than in soil from shrub interspaces. This stands in contrast to the findings of a companion study, in which two species of annual grasses grown in *Ambrosia* shrub-mound soil from the study site achieved about twice the biomass of those grown in interspace soil (H. Parag and C. Holzapfel, personal communication).

As predicted by hypothesis (2), *Acamptopappus* shrubs had less negative effects on associated *Ambrosia* seedlings than did *Ambrosia* shrubs (Fig. 2). In greenhouse experiments, soil from *Acamptopappus* shrub mounds inhibited growth of *Ambrosia* seedlings, possibly because it contained allelochemicals or soil pathogens. If similar effects occurred in the field, then other factors, such as shading or root interactions, have to account for the fact that *Ambrosia* seedlings were more negatively affected by *Ambrosia* than by *Acamptopappus* shrubs.

Interactions between mature shrubs

The presence of conspecific nearest neighbors inhibited growth of *Ambrosia* shrubs over the four-year study period (Table 2). This supports hypothesis (3) that interactions between mature *Ambrosia* shrubs were predominantly negative. However, as in a previous study of this species (Fonteyn and Mahall 1978, 1981), we found no effect of removing conspecific neighbors on Ψ s of *Ambrosia* during the first two growing seasons after the removal (Fig. 3). *Ambrosia* roots may have been slow in taking advantage of the soil space made available by the removal of neighboring shrubs. Such a slow response could have been caused by spatial segregation of their root systems (Schenk et al. 1999) brought about by the root-contact inhibition found in this species (Mahall and Callaway 1991, 1992, 1996). Plants that have root systems which are segregated from those of neighbors may be slow in their response to neighbor removals, because few of their roots would be initially present in the soil

space previously occupied by roots of the neighbor. Alternatively, it is possible, that Ψ s in *Ambrosia* are simply not good measures for soil water availability. Disequilibria between Ψ s and soil water potentials have been documented for other desert shrub species (Donovan et al. 1999; Ourcival and Berger 1995).

Ambrosia was affected by conspecific neighbors, but not by *Acamptopappus* neighbors (Figs. 3, 4; Table 2). This difference corresponds to spatial patterns in the community, where *Ambrosia* was spatially aggregated with *Acamptopappus* but spatially segregated from conspecifics (Schenk 1998). *Acamptopappus* shrubs were affected by *Ambrosia* neighbors both positively and negatively, apparently depending on climatic conditions (Fig. 3C) and on the position of the nearest neighbor (Fig. 4). As predicted by hypothesis (4), *Acamptopappus* shrubs may benefit to some degree from being on the more shaded northern side of *Ambrosia* neighbors, which may compensate for negative effects of having a competitor in close vicinity. *Ambrosia* shrubs cast little shade on the canopies of mature, equally tall *Acamptopappus* neighbors, but they can shade the lower parts of their neighbors and the soil in which these grow. During the fall-to-spring growing season, soil surfaces at the northern edge of *Ambrosia* canopies have lower temperatures than open areas or areas at the southern edge of *Ambrosia* shrubs during much of the day (Schenk 1998). *Acamptopappus* neighbors may benefit from this, as soil evaporation rates would be lower in the shade. Any improvement in water relations could potentially benefit *Acamptopappus* at this study site, because the mean annual rainfall there (130 mm) is about the lowest this species experiences in its range, as is evident from its geographic distribution (Lane 1988). In addition, temporary improvements in the water status of *Acamptopappus* shrubs may be due to uptake of water leaking out from *Ambrosia* roots at night. *Ambrosia* roots have been found to hydraulically redistribute water from moist to dryer parts of the soil (Yoder and Nowak 1999). Excavations of root systems at the study site suggest that both species tend to have similar maximum rooting depths of 1–1.5 m, suggesting that both have similar access to water stored at depth. However, *Ambrosia* neighbors positively affected the water status of *Acamptopappus* shrubs in spring 1997 (Fig. 3C), but not vice versa, which suggests that differences in root-system architecture and / or root anatomy may cause *Ambrosia* roots to be more prone to hydraulic redistribution than those of *Acamptopappus*.

Relationships between pattern and process

Studies of spatial patterns and plant demography in other desert ecosystems have suggested that the spatial structure of desert communities can be strongly affected by complex, positive and negative plant interactions (e.g., Ackerman 1979; McAuliffe 1988; Miriti et al. 1998; 2001), but few studies have experimentally tested links

between plant interactions and spatial community structure in deserts (Fonteyn and Mahall 1981; Holzapfel and Mahall 1999; Walker et al. 2001). Our study provides experimental support for a direct effect of plant interactions on the spatial structure of a desert community. Negative associations, such as the spatial segregation observed among *Ambrosia* shrubs corresponded to negative interactions found between these shrubs and also between these shrubs and their seedlings. Positive associations, such as the spatial aggregation of seedlings and of *Acamptopappus* shrubs on the northern side of *Ambrosia* shrubs corresponded with positive effects that shading had on seedling emergence (Schenk 1998) and that *Ambrosia* shrubs had on *Acamptopappus* neighbors. However, interactions between shrubs of the two species were complex. The directional association between these two species appears to be due to the fact that negative interactions with *Ambrosia* shrubs affect *Acamptopappus* neighbors unless they happen to be located on the northern side of *Ambrosia*, in which case positive effects of shading may alleviate negative effects of competition. Thus, the positive and directional association between these two species is probably brought about by a combination of positive and negative interactions, which may differ depending on the life stages involved and depending on the spatial arrangement of the neighbors.

The results of this study remind us that there is more than one dimension to the spatial ecology of plants. This may seem self-evident because the term "spatial" suggests three-dimensionality. But in fact the majority of ecological, spatial pattern analyses reduce spatial patterns to a single dimension, namely the distance between individual organisms (Dale 1999; Diggle 1983; Tilman and Kareiva 1997). Here we show that abiotic factors and interactions between organisms can also affect patterns in the second dimension of the direction between organisms. Because there have been few studies of directional patterns in plant communities (Aradóttir et al. 1997; Carlsson and Callaghan 1991; Valiente-Banuet et al. 1991; Valiente-Banuet and Ezcurra 1991) it is difficult to say at present whether two-dimensional patterns such as those discussed here may be rare, common, or ubiquitous. However, it is likely that such patterns exist in any environment where abiotic factors such as slope, soil gradients, wind, or solar radiation are strongly directional and where these factors affect resources that limit reproduction, dispersal, growth, or survival. As this study shows, directional abiotic factors can also cause biotic interactions to be directional and together affect the structure of a plant community in two dimensions.

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