

Spatial ecology of a small desert shrub on adjacent geological substrates

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Summary

1 Spatial pattern analyses were used to generate hypotheses about the processes that shape the structure of a plant community in the Mojave Desert of North America, with a focus on the semi-shrub *Ambrosia dumosa*. We analysed spatial distributions and sizes of this species relative to other semi-shrubs, shrubs and annuals, and the relationships between spatial patterns and abiotic and biotic habitat characteristics.

2 The analyses were based on maps of sample plots placed along a transect spanning two adjacent geological substrates: aeolian sand and gravelly, sandy to loamy alluvium. Of these two substrates, sand supported higher total biomasses of *Ambrosia* and of all woody perennials, while alluvium supported on average higher biomasses of winter annuals.

3 Annuals and seedlings of *Ambrosia* were much more strongly aggregated with *Ambrosia* canopies on sand than on alluvium, suggesting that these small plants were more strongly facilitated by *Ambrosia* on sand than on alluvium.

4 *Ambrosia* semi-shrubs were spatially segregated on sand but aggregated on alluvium, and the degree of segregation on sand increased with the total above-ground biomass of *Ambrosia* per unit area, indicating that negative interactions between *Ambrosia* plants were stronger in more productive habitats. Canopy sizes of *Ambrosia* in all mapped plots increased with distance to the nearest conspecific neighbour, which suggests that neighbour interactions negatively affected plant sizes.

5 *Ambrosia* plants on sand were spatially aggregated with *Acamptopappus sphaerocephalus* semi-shrubs, suggesting that at least one of these species may benefit from the association. *Ambrosia* plants were spatially segregated from *Larrea tridentata* shrubs on both substrates, possibly due to negative effects of *Larrea* roots on *Ambrosia* roots reported in previous studies.

6 Subtle differences in substrate characteristics were correlated with strong differences in the spatial distribution of *Ambrosia* plants relative to their neighbours, which suggests that edaphic conditions may affect the spatial structure of the community by modifying complex positive and negative interactions between neighbouring plants.

Key-words: *Ambrosia dumosa*; desert annuals; habitat quality; positive and negative plant interactions; replicated maps; soil texture; scale-dependent spatial patterns.

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Introduction

The spatial structure of a plant community observed at any point in time is the product of many processes in its past. These include biotic processes, such as plant dispersal, growth, mortality and herbivory, as well as other factors and processes, such as substrate, topography, climate, fire, disturbance, or land-use

history. More often than not, spatial patterns in the structure of a plant community will be the product of complex and interacting processes. The processes that are most important for shaping community structure are likely to leave observable imprints in spatial community structure. It should be possible therefore to use spatial pattern analyses in order to generate testable hypotheses about the processes that shape community structure.

The subject of this study was *Ambrosia dumosa* (A. Gray) Payne (Asteraceae), a drought-deciduous semi-shrub that is a very widespread and often dominant species in the Mojave and Sonoran Deserts of North America (Shreve 1925; Turner *et al.* 1995). We examined its spatial distributions and its sizes relative to conspecific neighbours as well as neighbours of different plant growth forms on two adjacent geological substrates in the western Mojave Desert. Effects of abiotic and biotic factors on spatial patterns were examined by analysing replicated, completely mapped, spatial samples, adopting an approach developed by Diggle *et al.* (1991). This study differs from previous spatial pattern analyses in plant ecology in that it was designed to test whether patterns differed between habitats or were correlated with other biotic and abiotic variables, instead of testing whether patterns deviated from null models of complete spatial randomness (e.g. Pielou 1977; Diggle 1983; Dale 1999). The replicated-maps technique was adopted because (i) deviations from randomness are the rule rather than the exception in spatial community structure (Greig-Smith 1979; Hutchings 1997), (ii) it allows examination of specific hypotheses about community structure based on mechanisms or ecological theory, and (iii) replication in general allows one to make inferences about a whole plant community or landscape, instead of just describing patterns in the plots that were actually sampled.

The underlying assumption of our study was that habitat quality affects plant performance and therefore the nature and intensity of interactions between neighbouring plants. Recent studies suggest that the nature of plant interactions may differ predictably between otherwise comparable habitats of lower and higher plant productivity. Interactions can have positive and negative effects on plant neighbours, often simultaneously, resulting either in net-positive or net-negative effects (Holzapfel & Mahall 1999). The relative importance of positive and negative interactions between plants appears to depend in part on habitat quality (Callaway & Walker 1997; Brooker & Callaghan 1998; Goldberg *et al.* 1999). Net positive plant interactions are most often found in habitats with high degrees of abiotic stresses and low productivity, and it has been postulated that this may be because interactions with plant neighbours can buffer effects of abiotic stress (Bertness & Callaway 1994; Callaway & Walker 1997; Brooker & Callaghan 1998). In contrast, net negative plant interactions occur in all kinds of habitats (Goldberg & Novoplansky 1997; Newman 1973;

Tilman 1988; Goldberg *et al.* 1999), although Grime (1973) proposed that they may be more intense in more productive habitats that have a lower degree of abiotic stress.

If these generalizations apply to the study system, spatial patterns that are indicative of net negative interactions should be more pronounced on the substrate on which plants are more productive. Two kinds of spatial patterns are thought to be indicators of such net negative interactions: (i) spatial segregation (i.e. 'regular' distribution) of individual plants (Fowler 1986; Phillips & MacMahon 1981; Rejmánek & Lepš 1996; Pacala 1997), and (ii) positive correlations between the distances separating nearest neighbours and the combined sizes of these neighbours (Pielou 1960). We tested the hypothesis that these two kinds of spatial patterns are more pronounced in habitats where plants are more productive. Interactions between *Ambrosia dumosa* and its neighbours at the same site were also studied experimentally (Holzapfel & Mahall 1999; Schenk & Mahall 2002), which allowed us to relate patterns to processes.

Materials and methods

STUDY SITE AND SAMPLING DESIGN

The study site is located in north-eastern Fremont Valley, California, at the western edge of the Mojave Desert (35°23' N, 117°41' W). The climate is arid, with on average more than 85% of precipitation falling between October and May. Mean annual precipitation is approximately 120 mm with high variability from year to year. Geological substrates of the study sites include aeolian deposits of Cajon sand of Holocene age and highly eroded alluvial Randsburg-Muroc soils of Pleistocene age (Hulin 1925; Dibblee 1952; Valverde & Hill 1981). The alluvium consists of gravelly, sandy loams, derived from weathered granitic rock, and is very heterogeneous. In the remainder of this paper, the two substrates will simply be denoted as sand and alluvium, respectively.

The vegetation is Mojave creosote-bush scrub (Barbour & Major 1988), dominated by the evergreen shrub species *Larrea tridentata* and the drought-deciduous semi-shrub *Ambrosia dumosa*, and on sandy substrate codominated by the drought-deciduous semi-shrub *Acamptopappus sphaerocephalus* (A. Gray) A. Gray var. *hirtellus* S. F. Blake (Asteraceae) (all nomenclature follows Hickman 1993). All perennials are hereafter referred to by their generic names. Both *Ambrosia* and *Acamptopappus* are semi-shrubs (also known as subshrubs or dwarf shrubs) that never reach heights above one metre, while *Larrea* is a shrub that can reach heights exceeding 2 m at the study site. The annual community consists mostly of winter annuals (for species see Table 1). Growing seasons typically last from the first major rainfall after the dry summer season until spring of the following year.

Table 1 Mean (± 1 SE) density (plants ha⁻¹), percentage cover and biomass of plants on mapped 400 m² plots of the two substrate types: sand (6 plots) and alluvium (4 plots). Values denoted with different letters are significantly different between substrate types at $P < 0.05$ (two-tailed t -tests)

	<i>Ambrosia</i>	<i>Acaemtopappus</i>	<i>Larrea</i>	All perennials*	All annuals†
Density (ha ⁻¹)					
Sand	2375 ^a \pm 382	1792 ^a \pm 521	256 ^a \pm 36		
Alluvium	2100 ^a \pm 344	0 ^b \pm 0	335 ^a \pm 49		
Cover (%)					
Sand	10.1 ^a \pm 1.6	5.4 ^a \pm 0.9	7.9 ^a \pm 0.8	23.9 ^a \pm 1.4	
Alluvium	5.0 ^b \pm 0.5	0.0 ^b \pm 0.0	12.9 ^b \pm 1.3	18.1 ^b \pm 1.1	
Biomass (g m ⁻²)					
Sand	140 ^a \pm 23	85 ^a \pm 11	99 ^a \pm 9	327 ^a \pm 16	47 ^a \pm 4
Alluvium	69 ^b \pm 7	0.0 ^b \pm 0.0	177 ^b \pm 17	247 ^b \pm 13	58 ^b \pm 7

*Other perennial species occurring in small numbers included *Achnatherum hymenoides* (Roemer & Schultes) Barkworth, *Hymenoclea salsola* A. Gray, *Krascheninnikovia lanata* (Pursh) A.D.J. Meeuse & Smit, *Ericameria cooperi* (A. Gray) H.M. Hall, *Mirabilis bigelovii* A. Gray, *Psoralea arborescens* (A. Gray) Barneby and *Senna armata* (S. Watson) H. Irwin & Barneby. †Common species of winter annuals: on all substrates: *Schismus barbatus* (L.) Thell., *Bromus madritensis* L. ssp. *rubens* (L.) Husnot, *Erodium cicutarium* (L.) L'Hér., *Cryptantha* spp., *Amsinckia tessellata* A. Gray. Only on sand: *Chaenactis fremontii* A. Gray, *Camissonia campestris* (E. Greene) Raven, and *Eriophyllum wallacei* (A. Gray) A. Gray; only on alluvium: *Lasthenia californica* DC., *Tropidocarpum gracile* Hook.

Table 2 Edaphic characteristics of the two substrate types at the study site, sand (6 plots) and alluvium (4 plots). Soil profiles were studied in pits adjacent to the mapped plots. Nitrogen and carbon data are for the 5–30 cm depth interval based on 10 samples per microsite (open area or edge of *Ambrosia* semi-shrubs) for each mapped plot. Organic carbon and total nitrogen contents were determined using a Carlo Erba CN analyser (model NA 1500 NC). Carbonates were removed from the soil by the HCl vapour acidification method (Hedges & Stern 1984)

	Sand	Alluvium
Elevation (m)	707–844 m	878–942 m
Slope (%)	2.7–4.1	4.5–7.1
Aspect	WSW–WNW	NW–NNW
Soil texture (%; 0–1.2 m)	Silt: 9.2–12.5 Clay: 2.3–4.1	Silt: 13.7–18.5 Clay: 11.2–11.7
Rocks and gravel (volume percentage; 0–1.2 m)	14.8 \pm 2.7	47.4 \pm 6.8†
Nitrogen (g kg ⁻¹ of dry soil)		
Open areas	0.10 \pm 0.01	0.27 \pm 0.01
Under semi-shrubs	0.14 \pm 0.01	0.44 \pm 0.06
Organic carbon (g kg ⁻¹ of dry soil)		
Open areas	0.84 \pm 0.03	2.13 \pm 0.14
Under semi-shrubs	1.28 \pm 0.12	3.54 \pm 0.59
Soil classification (US soil taxonomy)	Typic Torripsamments	Typic to calcic Petrocalcids, typic Haplocalcids, typic Torriorthents

Ten 20 \times 20 m plots (hereafter referred to as the mapped plots) were placed on the north-west facing slope of the Rand Mountains along a 5.6-km long east–west transect, spanning an elevational gradient ranging from 707 m to 942 m. Six plots were located on sand and four on alluvium. Edaphic characteristics of these two substrates are summarized in Table 2.

All live and dead perennial plants were mapped between April 1995 and May 1997 using a total station transit (model GTS-3B, Topcon, Paramus, New Jersey). For live plants, two canopy diameters, representing the maximum extent of the living canopy in the north–south and east–west direction and maximum canopy height, were measured.

Spatial distributions of emerging seedlings of perennials were measured after a germination event following

early fall rains in 1997. *Ambrosia* semi-shrubs on sand and alluvium ($n = 20$ each) were randomly chosen, and distances to their canopy edge were recorded for all seedlings closer to these shrubs than to other woody plants. In addition, on each substrate, 30 circular plots of 1-m² area were randomly placed in open areas, and all seedlings within these plots were counted.

Above-ground biomass of shrubs and semi-shrubs per unit area (i.e. biomass density) was estimated for all 10 mapped plots using allometric regressions between canopy dimensions and above-ground shrub biomass (see Appendix). Above-ground biomass of winter annuals under the canopy edges of *Ambrosia* semi-shrubs, and in an adjacent open area, was measured in two of the mapped plots on each substrate during spring 1995, 1996, 1997 and 1998. Details about the

sampling designs for biomass of annuals and perennials may be found in the appendix.

DATA ANALYSIS

Spatial association of annuals and Ambrosia seedlings with Ambrosia semi-shrubs

To analyse spatial relationships between *Ambrosia* semi-shrubs and annual plants, we calculated the ratio of biomass density (in g m⁻²) at canopy edge (mean of N-, E-, S-, W-edges) to biomass density of annuals in adjacent open areas for each *Ambrosia* semi-shrub sampled. Ratios were log-transformed to normalize the distributions and analysed in a nested design ANOVA, with substrate and year as independent factors. The two mapped plots for which data on annual biomass were collected were nested in each substrate, and replicate shrubs were nested within mapped plots.

Spatial distribution of Ambrosia relative to shrubs and semi-shrubs

To analyse spatial relationships between *Ambrosia* semi-shrubs and other woody plants, including conspecifics, *Larrea* shrubs, and *Acamptopappus* semi-shrubs, we calculated intraspecific and interspecific *K*-functions (Ripley 1976; Diggle 1983). *K_i(r)* is the ratio between the number of plants (regardless of size) counted within distance *r* around an individual plant *i* growing at a location *s* and the spatial intensity $\lambda(s)$ (i.e. the local density) at that location, and it has the dimension of area. Spatial intensities $\lambda(s)$ for all locations within a mapped plot *j* were approximated by mean plot density *d_j* (Diggle 1983). For each mapped plot *j*, empirical, mean $\hat{K}_j(r)$ -functions were calculated by computing mean *K(r)*-values for individual plants for distances *r* increasing from 0.2 m to 5 m in 0.2 m increments, using the geometric edge correction described by Diggle (1983) to correct *K(r)*-values for plants near the edge of mapped plots.

To test for differences in spatial distributions of perennial plants between the two substrate types (alluvium and sand) we used the 20 × 20 m plots (six on sand, four on alluvium) as ‘treatment’ replicates. The experimental design was that of a comparative mensurative experiment, where replicates within ‘treatments’ (i.e. substrates), although separated in space, can be considered to be true replicates (Hurlbert 1984). The replicate $\hat{K}_j(r)$ functions for individual mapped plots were combined into mean, weighted $\hat{K}_{mean}(r)$ functions (Diggle *et al.* 1991) for each substrate type. For each substrate and species combination, these values were calculated for each 0.2 m r-increment as

$$\hat{K}_{mean}(r) = \sum_{j=1}^m w_j \hat{K}_j(r) \quad \text{eqn 1}$$

where, for intraspecific analyses, the weight *w_j* is the number of plants of species *A* in plot *j* divided by the

total number of plants of species *A* in all *m* plots on this substrate type. For analyses of interspecific spatial patterns, we calculated the weights as

$$w_j = \sqrt{n_{j,A}n_{j,B}} / \sum_{j=1}^m \sqrt{n_{j,A}n_{j,B}} \quad \text{eqn 2}$$

where *n_{j,A}* and *n_{j,B}* are the number of plants of species *A* and *B*, respectively, in plot *j*.

To test whether the observed $\hat{K}_{mean}(r)$ -values deviated significantly from a null-model of complete spatial randomness, we employed a Monte Carlo technique modified from Lotwick & Silverman (1982) and Diggle (1983). One-thousand $\hat{K}_{mean}(r)$ -functions for random point patterns were generated for each substrate type using equations 1 and 2 and using the same plot sizes and densities as in the mapped plots. Observed $\hat{K}_{mean}(r)$ -values were considered to indicate significant (*P* < 0.05) spatial aggregation when they were greater than the upper 97.5-percentile of the random $\hat{K}_{mean}(r)$ -values for the same *r*-interval and spatial segregation when they were lower than the lower 97.5-percentile of the random $\hat{K}_{mean}(r)$ -values for that interval.

$\hat{K}_{mean}(r)$ -functions were compared to see whether the positions of *Ambrosia* relative to *Ambrosia* (intra-specific spatial patterns) and *Ambrosia* relative to *Larrea* (interspecific spatial patterns) differed between substrate types (*Acamptopappus* occurred with *Ambrosia* only on sand). Because of the relatively low number of replicates, the unknown statistical properties of $\hat{K}_j(r)$, and the non-independence among consecutive $\hat{K}_j(r)$ -intervals, we employed the following Monte Carlo randomization procedure to determine whether observed differences between $\hat{K}_{mean}(r)$ -functions were statistically significant.

For each 0.2 m *r*-interval, differences in $\hat{K}_{mean}(r)$ between substrates were considered to be significant only if the four replicates for alluvium were either all lower or all higher than the six replicates for sand. The probability of this outcome for each individual 0.2 m *r*-interval is *P* = 0.0105 (Kruskal–Wallis test). The probability of finding such an outcome once or a few times is obviously very high when patterns are compared over all 250.2 m *r*-intervals. However, differences in spatial patterns are more likely to reflect underlying ecological processes that are important for structuring a community if they occur over a larger range of scales than individual 0.2 m distance intervals. For this reason, we looked for instances where a number of consecutive *r*-intervals differed significantly (as defined above) between treatments and then determined the likelihood of finding such a number of consecutive, significantly different intervals among randomly generated $\hat{K}_{mean}(r)$ functions.

This was done by generating 10 random $\hat{K}_j(r)$ functions using the same plot sizes and densities as for the mapped plots and grouping them into two categories, representing random functions for the treatment ‘sand’ (*n* = 6) and for the treatment ‘alluvium’ (*n* = 4).

This whole procedure was repeated 1000 times, while each time calculating the number of consecutive r -intervals that differed significantly between the two treatments. Using this procedure, we could determine the likelihood of finding any number of consecutive significantly different $\hat{K}_j(r)$ -intervals between six randomly generated $\hat{K}_j(r)$ replicates for one treatment and four randomly generated $\hat{K}_j(r)$ replicates for another treatment.

For graphs, tables, and statistical tests $\hat{K}(r)$ -values were converted to:

$$J(r) = \frac{\hat{K}(r)}{\pi r^2} - 1 \quad \text{eqn 3}$$

$J(r)$ is a scale-dependent spatial distribution index that is equal to zero for completely random patterns. It was chosen because it is ecologically more meaningful than other commonly used conversions of $\hat{K}(r)$ (e.g. Diggle 1983; Bailey & Gatrell 1995), being a simple measure of relative density. For example, a positive value of 0.2 for a given distance r indicates that, on average, 20% more plants were counted in a circular area of radius r around the average individual plant than expected if the pattern were random.

Effects of neighbours on canopy sizes of *Ambrosia*

To explore effects of neighbours on canopy sizes of *Ambrosia* we used size-distance analyses (Pielou 1960). For each individual *Ambrosia* in the mapped plots we calculated sizes of and distances to each nearest neighbour of the species *Ambrosia*, *Larrea* and *Acamptopappus* (only on sand). Analyses were restricted to nearest neighbours within 3 m for semi-shrubs and within 5 m for *Larrea* shrubs to account for differences in maximum lateral root spreads between semi-shrubs and shrubs (Schenk & Jackson 2002). Neighbours other than the nearest ones were not included in these analyses because exploratory analyses had found no significant relationships between such neighbours and *Ambrosia* sizes (data not shown). To enable comparisons between mapped plots, in which mean canopy sizes were different, canopy biomasses for each species were standardized within mapped plots by dividing the biomass of each individual plant by the mean canopy biomass found for the same species in the same mapped plot. Size-distance relationships for conspecific *Ambrosia* neighbours were analysed by linear regression of their summed canopy biomasses against distances between them. Size-distance relationships for *Ambrosia*/*Acamptopappus* neighbour pairs and *Ambrosia*/*Larrea* neighbour pairs were analysed by linear regression of *Ambrosia* biomasses against distances to neighbours and biomasses of the neighbours. Differences in size-distance relationships between substrates were analysed in nested design ANOVAs with standardized *Ambrosia* biomass as dependent variable, substrate and distance as independent factors, and mapped plots nested in each substrate.

Relationships between spatial indices and other ecological factors

To explore relationships between spatial patterns and the ecological conditions of the mapped plots, we calculated Pearson correlation coefficients for the linear relationships between spatial indices, $J(r = 1 \text{ m})$ and $J(r = 2 \text{ m})$, and elevation, slope, aspect, volume percentage of rocks and gravel, clay percentage, as well as biomass density of *Ambrosia*, *Acamptopappus*, *Larrea*, all woody perennials, and ground area per unit biomass of *Ambrosia*.

Results

ECOLOGICAL CONDITIONS ON THE TWO SUBSTRATES

Mapped plots on alluvium were located at higher elevations and on slightly steeper slopes than those on sand (Table 2). Alluvium plots mostly faced north-west, while plots on sand mostly faced west. The soil on alluvium contained much higher percentages of gravel and rock, while the texture of the bulk soil on sand was coarser than on alluvium. Other abiotic characteristics of the two substrates are listed in Table 2.

Several biotic variables that may affect the spatial ecology of *Ambrosia* also differed between the two substrates. Above-ground biomass of all woody plants per unit area was *c.* 32% higher ($P < 0.01$), and that of all semi-shrubs more than 200% higher ($P < 0.0001$) on sand than on alluvium (Table 1). *Larrea* biomass density was *c.* 80% higher on alluvium than on sand ($P < 0.01$). Mortality rates of woody plants may differ between the substrates, because on alluvium 17.3% of all semi-shrubs were dead, while on sand 33.3% were dead ($P < 0.01$). Peak biomass density of winter annuals was on average *c.* 25% higher on alluvium ($P < 0.001$, Fig. 1), with the largest differences in

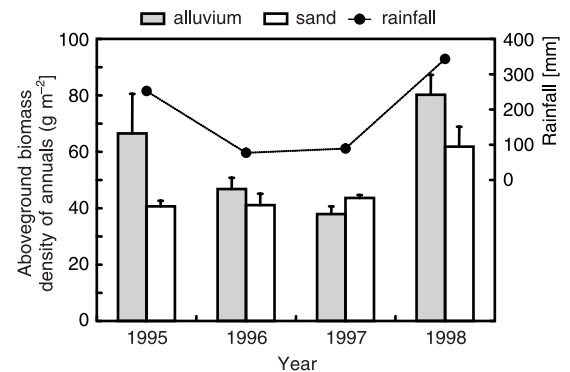


Fig. 1 Mean above-ground biomass of winter annuals estimated for 400-m² mapped plots, including annuals in open areas and under canopies of woody perennials, measured as biomass density at the peak of the growing season during late spring of the years 1995–98. Rainfall data are totals for the growing season (September of the previous years to August of the current year).

Table 3 Spatial aggregation of winter annuals with *Ambrosia* canopies, as measured by the ratios of the above-ground biomass density of annuals at the edge of *Ambrosia* canopies to above-ground biomass density of annuals in adjacent open areas. Biomass of annuals was measured in spring of four consecutive years at the peak of each growing season. According to nested-design ANOVA, differences between substrates (d.f. = 1, mean square = 20.83, *F*-ratio = 205.2), between years (d.f. = 3, mean square = 10.36, *F*-ratio = 102.1), between mapped plots (nested within substrates; d.f. = 2, mean square = 0.95, *F*-ratio = 9.4), and the interactions between year and substrate (d.f. = 3, mean square = 4.51, *F*-ratio = 44.4), were all statistically significant at $P < 0.001$

Growing season	Rainfall (mm)	Sand		Alluvium	
		Ratio	<i>n</i>	Ratio	<i>n</i>
1994/95	252	3.16 ± 0.08	196	1.44 ± 0.05	103
1995/96	77	1.28 ± 0.06	90	1.13 ± 0.04	75
1996/97	89	1.57 ± 0.03	69	1.15 ± 0.03	55
1997/98	343	1.72 ± 0.05	60	1.23 ± 0.04	60
Mean	190	1.93 ± 0.42		1.24 ± 0.07	

biomass between the substrates found in the two wet years 1995 and 1998.

SPATIAL ASSOCIATION OF ANNUALS WITH *AMBROSIA*

Peak biomass densities of annuals in all years on both substrates were significantly higher under the canopy edges of *Ambrosia* semi-shrubs than in open areas ($P < 0.01$), and this difference was more pronounced on sand than on the alluvium ($P < 0.001$; Table 3). Annuals associated with *Ambrosia* canopies had on average *c.* 27% higher biomass density on sand than on alluvium, but annuals in open areas had on average *c.* 32% higher biomass density on alluvium than on sand. The ratio between annual biomass density at *Ambrosia* canopy edges to that in adjacent open areas, which is a measure for the spatial aggregation of annuals with *Ambrosia* semi-shrubs, was highest in the relatively wet year 1995 (252 mm of rainfall) on both substrate types (Table 3). There was no significant relationship between the spatial aggregation of annuals with *Ambrosia* semi-shrubs and rainfall totals or with the total biomass density of annuals.

On sand, larger *Ambrosia* plants had much higher biomass densities of annuals at their canopy edge than smaller plants (Fig. 2), but sizes of *Ambrosia* had no effects on biomass density of annuals in open areas adjacent to the *Ambrosia* plants. No significant relationship between *Ambrosia* size and biomass density of associated annuals was found on alluvium (Fig. 2).

SPATIAL ASSOCIATION BETWEEN SEEDLINGS AND *AMBROSIA*

Total *Ambrosia* seedling densities per unit area were similar for both substrates (*c.* 3.25 m⁻²), but on sand, 84% of all seedlings were located within ± 0.2 m of an

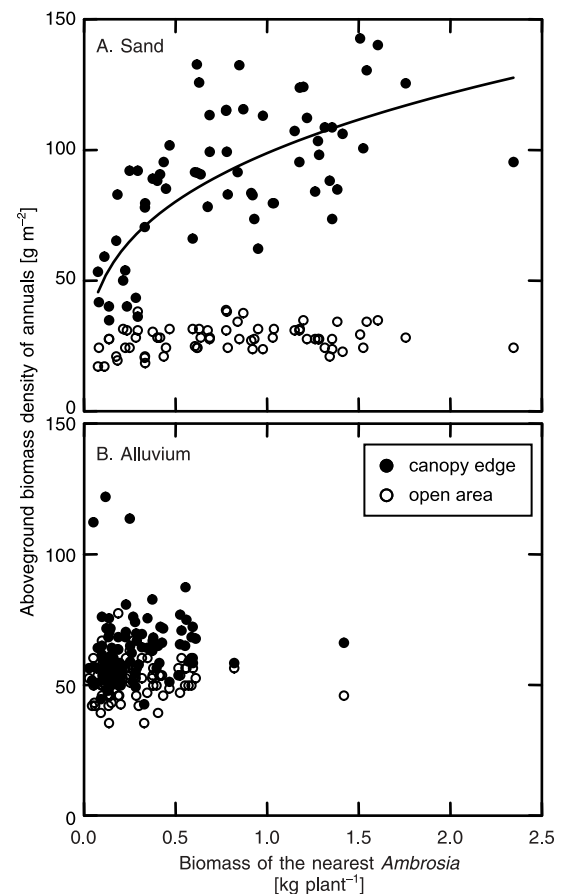


Fig. 2 Biomass density of winter annuals at the peak of the 1994/95 growing season in spring 1995. Biomass of annuals was measured in 10 × 10 cm quadrats placed either at the canopy edge of *Ambrosia* semi-shrubs or in open areas adjacent to *Ambrosia* semi-shrubs, and is shown as a function of the biomass of the closest individual *Ambrosia* plants. The curve in graph A depicts a regression curve of the type $y = a + b \ln x$, with $r^2 = 0.479$ ($P < 0.001$). No other significant regressions were found for relationships between biomass densities of annuals and biomasses of the closest *Ambrosia* semi-shrubs.

Ambrosia canopy, while on alluvium 88% of all seedlings were in open areas. Densities of *Ambrosia* seedlings within ± 0.2 m of *Ambrosia* canopy edges were extremely variable, but tended to be higher on alluvium (81 ± 28 m⁻²) than on sand (35 ± 6 m⁻²; difference n.s.). Densities in open areas were more than 10 times higher ($P < 0.001$) on alluvium (3.2 ± 0.9 m⁻²) than on sand (0.3 ± 0.1 m⁻²). Spatial aggregation of *Ambrosia* seedlings with *Ambrosia* canopies, expressed as the ratio between density at canopy edge to density in the open, was therefore more than 5 times higher on sand than on alluvium. Seedlings of other perennial species were found only in small numbers.

SPATIAL DISTRIBUTION OF *AMBROSIA* RELATIVE TO OTHER PERENNIALS

Ambrosia semi-shrubs on sand were intraspecifically segregated ($J(r) < 0$; $P < 0.05$) at spatial scales of less

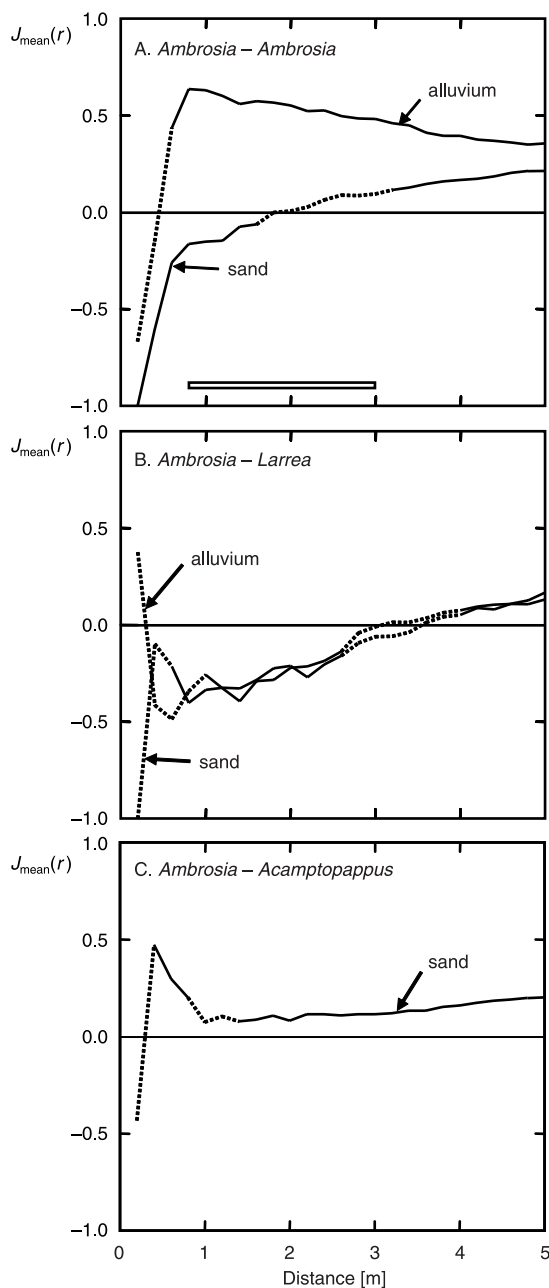


Fig. 3 Scale-dependent spatial patterns in the distribution of *Ambrosia dumosa* relative to its neighbours on sand (6 mapped plots) and alluvium (4 mapped plots). Mean spatial distribution indices, $J_{\text{mean}}(r)$ (see eqn 3), for the two substrate types are depicted. Dotted parts of the lines are not significantly ($P < 0.05$) different from complete spatial randomness, whereas continuous parts of the lines indicate significant spatial aggregation where $J_{\text{mean}}(r) > 0$, or spatial segregation where $J_{\text{mean}}(r) < 0$. The horizontal bar in graph A shows the range of distances over which $J_{\text{mean}}(r)$ values differed significantly ($P < 0.05$) between substrates.

than 1.6 m and weakly aggregated at larger scales of more than 3.4 m (Fig. 3a). In contrast, *Ambrosia* semi-shrubs on alluvium were strongly aggregated ($J(r) > 0$; $P < 0.05$) at all scales from 0.4 m to 5 m (Fig. 3a). The $J(r)$ -values for *Ambrosia* on the two substrates were significantly different ($P < 0.05$) for the 11 consecutive 0.2 m distance intervals between 0.6 m and 3.0 m

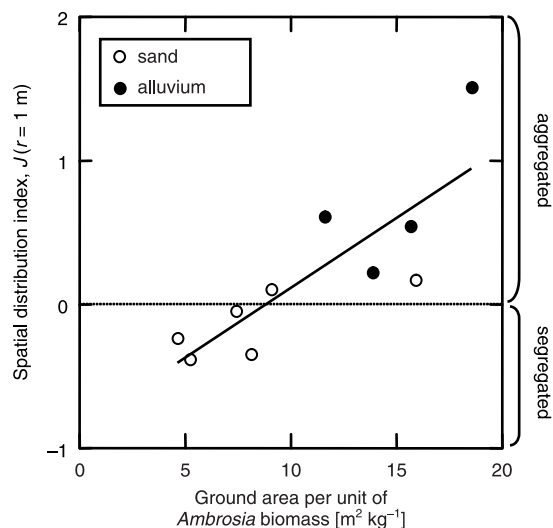


Fig. 4 Intraspecific, small-scale, spatial patterns of *Ambrosia dumosa* as a function of the ground area per unit of above-ground biomass of *Ambrosia* (in $\text{m}^2 \text{kg}^{-2}$). Mean $J(r)$ -values for each plot were calculated for the distance of $r = 1$ m around individual plants for each mapped plot. The data were statistically analysed in a generalized linear model with $J(r = 1 \text{ m})$ as dependent variable, substrate as categorical variable, and ground area per unit of *Ambrosia* biomass as covariate. In this model ($r^2 = 0.816$), the effect of ground area per unit of *Ambrosia* biomass was significant (sum of squares 0.655, d.f. = 1, F -ratio = 7.364, $P = 0.035$) but the effect of substrate was not (sum of squares = 0.077, d.f. = 1, F -ratio = 0.864, $P = 0.389$). The interaction between these two variables also was not significant (sum of squares 0.180, d.f. = 1, F -ratio = 2.023, $P = 0.205$), indicating that the slopes of the relationships between $J(r = 1 \text{ m})$ and ground area per unit of *Ambrosia* biomass were not different between substrates. The linear regression fitted through all points was statistically significant with $r^2 = 0.685$ and $P = 0.003$.

(Fig. 3a). The likelihood of finding significant differences for 11 or more consecutive distance intervals, as determined by our bootstrap procedure, was $P = 0.001$.

An increase in the spatial distribution index $J(r)$ in response to an ecological variable signifies an increase in spatial aggregation or a decrease in spatial segregation. The spatial distribution index $J_{\text{AA}}(r)$ for intraspecific patterns of *Ambrosia* semi-shrubs on the scale of $r = 1$ around individual plants decreased significantly with the biomass density of *Ambrosia* (Table 4, Fig. 4) and with that of all woody perennials, but increased with *Larrea* biomass density, and was not significantly related to *Acamptopappus* biomass density (Table 4). It also increased with aspect of the mapped plot (from WSW to NNW) and the percentage of clay in the bulk soil (Table 4). The spatial distribution index $J_{\text{AA}}(2 \text{ m})$ at the scale of $r = 2$ m was negatively related to *Larrea* biomass density (Table 4). Both $J_{\text{AA}}(1 \text{ m})$ and $J_{\text{AA}}(2 \text{ m})$ were positively related to the ground area per unit of *Ambrosia* biomass (Fig. 4), indicating that spatial segregation increased as less space was available for each unit of *Ambrosia* biomass.

Larrea and *Ambrosia* were spatially segregated from each other at a scale of between 0.6 m and 2.6 m on

Table 4 Pearson correlation coefficients for the spatial indices, $J(r)$, for *Ambrosia dumosa* with edaphic and biotic variables of the 10 mapped plots. The spatial indices shown are for the distribution of *Ambrosia* relative to conspecific neighbours (J_{AA}), relative to *Larrea* neighbours (J_{AL}), and relative to *Acamptopappus* neighbours (J_{AP}). The spatial distribution indices J (1 m) and J (2 m) characterize spatial aggregation (if $J > 0$) or segregation (if $J < 0$) at the scale of 1- and 2-m distances around individual plants J (1 m) and J (2 m), respectively). Significant correlations, which were not adjusted for multiple comparisons, are marked by a single asterisk (*) for $P < 0.05$ or a double asterisk (**) for $P < 0.01$

Spatial index:	J_{AA} (1 m)	J_{AA} (2 m)	J_{AP} (1 m)	J_{AP} (2 m)	J_{AL} (1 m)	J_{AL} (2 m)
Sample size (number of mapped plots):	10	10	6	6	10	10
Elevation (m)	+0.59	+0.59	-0.35	-0.65	+0.09	-0.19
Slope (%)	+0.45	+0.37	-0.14	-0.65	+0.23	+0.05
Aspect (°)	+0.71*	+0.54	-0.47	-0.23	+0.02	-0.13
Rocks and gravel (volume percentage)	+0.63	+0.61	+0.78	+0.54	+0.23	-0.14
Clay (%)	+0.67*	+0.59	+0.08	+0.07	+0.12	-0.12
<i>Ambrosia</i> biomass (g m^{-2})	-0.72*	-0.58	+0.16	-0.33	+0.34	+0.12
<i>Acamptopappus</i> biomass (g m^{-2})	+0.51	-0.08	+0.21	+0.43	-0.15	+0.26
<i>Larrea</i> biomass (g m^{-2})	+0.75*	+0.75*	+0.61	+0.18	+0.11	-0.16
Total perennial biomass (g m^{-2})	-0.67*	-0.53	+0.67	-0.08	+0.30	+0.14
Area per <i>Ambrosia</i> biomass ($\text{m}^2 \text{g}^{-1}$)	+0.83**	+0.69*	-0.13	+0.34	-0.15	-0.20

sand (Fig. 3b), and between 1 m and 2.6 m on alluvium (Fig. 3b), and the shapes of the $J(r)$ -graphs for the two substrates were not significantly different. *Ambrosia* and *Acamptopappus*, which co-occurred only on sand, were aggregated with each other at spatial scales between 0.4 and 0.8 m and 1.4–5 m (Fig. 3c). The degree of interspecific aggregation or segregation of *Ambrosia* with *Larrea* or *Acamptopappus* was not significantly correlated with abiotic or biotic characteristics of the mapped plots (Table 4).

SIZE-DISTANCE ANALYSES OF NEAREST NEIGHBOURS

Summed biomasses of nearest *Ambrosia* neighbours were positively correlated with the distances between them in all mapped plots ($P < 0.0001$), and there was no significant difference in this effect between the two substrates (Table 5). On average, *Ambrosia* plants increased in biomass by about 60% for each metre distance to the nearest conspecific neighbour. The relationship between *Ambrosia* biomass and distance to the nearest *Larrea* shrub only bordered on significance ($P = 0.054$), and there was no effect of *Larrea* size and no difference between substrate types (Table 5). On sand, the biomass of *Ambrosia* semi-shrubs was significantly related to the distance to the nearest *Acamptopappus* neighbour, but not to its size (Table 5). However, canopy biomass of *Ambrosia* only increased by about 16% per meter distance to the nearest *Acamptopappus* semi-shrub.

Discussion

The goal of this study was to analyse spatial patterns in the locations and sizes of *Ambrosia* plants relative to their neighbours in order to investigate underlying processes that shape the spatial structure of these desert communities. *Ambrosia* plants can live for several hundred years (Turner 1990; Miriti *et al.* 2001),

which suggests that the spatial structure of *Ambrosia* populations may reflect processes compounded over long periods of time. We found several strong relationships between spatial patterns and abiotic and biotic habitat characteristics (summarized in Table 6). The habitats on the two substrates studied differed in elevation, slope, aspect, as well as in soil characteristics, and supported different biomasses of different species. It is therefore not possible to attribute differences in spatial patterns to any one cause. However, spatial patterns in the distribution of plants and plant sizes relative to their neighbours are most likely to be influenced by neighbour interactions. Substrate heterogeneity and topography are more likely to affect the precise locations and absolute sizes of plants (i.e. first order properties of spatial patterns; Bailey & Gatrell 1995), and less likely to affect the distribution and sizes relative to neighbours (i.e. second order properties of patterns). Differences in second-order properties of spatial patterns for *Ambrosia* in different habitats suggests that plant interactions were affected by habitat characteristics. This interpretation is supported by experimental findings on interactions between *Ambrosia* and its neighbours at the same study site (Holzapfel & Mahall 1999; Schenk & Mahall 2002).

ECOLOGICAL CONDITIONS ON THE TWO SUBSTRATES

The abiotic conditions of the two substrates appear to result in a water regime that is more favourable for plant growth on sand than on alluvium. The alluvium had more rocks on the soil surface and slightly steeper slopes, suggesting that surface runoff might be greater on alluvium than on sand. Moreover, in strongly water-limited environments, sandy soils tend to have a more favourable water regime for plant growth than fine-textured soils, because infiltration is deeper and surface evaporation rates are lower, as sandy surfaces tend to dry out more rapidly (Paulsen 1912; Alizai & Hulbert

Table 5 ANOVA tables for statistical analyses of size-distance relationships between *Ambrosia dumosa* semi-shrubs and (a) nearest conspecific neighbours within 3-m distance, (b) nearest *Acamptopappus sphaerocephalus* semi-shrubs within 3-m distance, and (c) nearest *Larrea tridentata* shrubs within 5-m distance. Plant sizes were characterized by above-ground biomasses, calculated from canopy dimensions using allometric relationships, and were standardized for each species within each sample (see Methods for details). Independent variables included substrate type (sand or alluvium, except for b), mapped plot (nested within substrate; 6 plots on sand, 4 on alluvium), and, in the case of interspecific relationships, standardized biomasses of *Acamptopappus* and *Larrea*, for b and c, respectively

(a) Size distance relationships between nearest neighbours of *Ambrosia dumosa*

Dependent variable	Summed biomass of nearest <i>Ambrosia</i> neighbours			
	Source	Sum of Squares	d.f.	F-ratio
Distance	65.815	1	83.561	< 0.0001
Substrate	2.060	1	2.616	0.106
Substrate × distance	0.535	1	0.680	0.410
Mapped plot	7.272	8	1.154	0.325
Error	471.005	598		

(b) Size distance relationships between nearest neighbours of *Ambrosia dumosa* and *Acamptopappus sphaerocephalus* (the latter species occurred only on sand)

Dependent variable	Biomass of <i>Ambrosia</i>			
	Source	Sum of Squares	d.f.	F-ratio
Distance	6.170	1	12.865	0.0004
<i>Acamptopappus</i> biomass	0.958	1	1.998	0.158
Mapped plot	0.783	5	0.327	0.897
Error	252.258	526		

(c) Size distance relationships between nearest neighbours of *Ambrosia dumosa* and *Larrea tridentata*

Dependent variable	Biomass of <i>Ambrosia</i>			
	Source	Sum of Squares	d.f.	F-ratio
Distance	1.604	1	3.726	0.054
Substrate	0.986	1	2.291	0.131
Substrate × distance	0.574	1	1.334	0.249
<i>Larrea</i> biomass	1.030	1	2.392	0.122
Mapped plot	1.109	7	0.368	0.921
Error	269.504	626	0.431	

Table 6 Summary of the spatial patterns observed for the distribution and sizes of *Ambrosia* semi-shrubs relative to their neighbours on the two geological substrates, sand and alluvium. The scale for the spatial relationships listed is that of the distances over which these plants are most likely to interact. These distances were estimated from data on median root spreads of annuals (0.10 m), semi-shrubs (0.70 m), and shrubs in deserts (2.10 m) (Schenk & Jackson 2002), as measured from the centre of each plant. The spatial patterns listed are the dominant ones found for the scales of interaction listed in this table. For details see Fig. 3 and the results section. The spatial scale of size-distance analyses varies with the distance to the nearest neighbour, but did not exceed the distances listed

Spatial relationships	Scale of interaction	Sand	Alluvium
Annuals with <i>Ambrosia</i>	0–0.8 m	Strongly aggregated	Weakly aggregated
<i>Ambrosia</i> with conspecific neighbours	0–1.4 m	Segregated	Aggregated
<i>Ambrosia</i> with <i>Larrea</i> shrubs	0–2.8 m	Segregated	Segregated
<i>Ambrosia</i> with <i>Acamptopappus</i> semi-shrubs	0–1.4 m	Aggregated	n.a.
Size-distance correlations between nearest <i>Ambrosia</i> neighbours	Variable, < 3 m	Positive	Positive
Size-distance correlations between nearest <i>Ambrosia</i> and <i>Larrea</i> neighbours	Variable, < 5 m	Not significant	Not significant
Size-distance correlations between nearest <i>Ambrosia</i> and <i>Acamptopappus</i> neighbours	Variable, < 3 m	Weakly positive	n.a.

1970; Hillel & van Bavel 1976; Smith *et al.* 1995). Elevation probably had a negligible effect on water availability on the two substrates, as local rainfall totals only increase by about 6 mm year⁻¹ per 100 m elevation.

SPATIAL ASSOCIATION OF ANNUALS AND SEEDLINGS WITH *AMBROSIA*

Winter annuals and *Ambrosia* seedlings were aggregated with *Ambrosia* semi-shrubs, which suggests that *Ambrosia* canopies offer a microhabitat favouring establishment of seedlings, as well as growth of many annual species. Biomass density of annuals at the edge of *Ambrosia* canopies was higher on sand than on alluvium, despite the much lower fertility of the sand (Table 2). Annuals establishing at the edge of *Ambrosia* canopies may have benefited from the more favourable water regime of the sand. In open areas, rapid drying of the sandy soil surface could be a major impediment to germination. In contrast, canopies shade the surface and increase soil water-holding capacity by adding plant litter and other organic materials, which may explain why, on sand, annuals and *Ambrosia* seedlings are much more likely to establish near *Ambrosia* canopies than in the open. These effects would be expected to be stronger under canopies of older and larger semi-shrubs. Such semi-shrubs do, in fact, support higher biomass densities of annuals on sand (Fig. 2).

Ambrosia semi-shrubs facilitate not only the establishment of annuals, but also their growth by providing a partly shaded and more fertile habitat (Holzapfel & Mahall 1999). In fact, the annuals tend to grow so well that *Ambrosia* semi-shrubs on sand were found to be negatively affected by them (Holzapfel & Mahall 1999). *Ambrosia* seedlings, however, were found to have a 20 times lower chance of surviving to the end of their second growing season when located next to a conspecific semi-shrub, rather than in open areas (Schenk & Mahall 2002). Similar negative effects of *Ambrosia* plants on their seedlings have been reported from other sites (Vasek 1979/80; Prose *et al.* 1987; Hunter 1989; Miriti *et al.* 1998; Walker *et al.* 2001). Thus, although these spatial aggregations of annuals and seedlings with *Ambrosia* canopies were probably initially caused by a net positive effect of the semi-shrubs on seedling emergence, they later caused negative interactions between the closely associated plants.

INTRASPECIFIC SPATIAL PATTERNS

The observed positive relationships between the sizes of *Ambrosia* neighbours and the distances between them suggest that sizes were negatively affected by interactions between the individual plants. This conclusion is supported by experimental findings from the study site, at least on sand, which have shown that removal of nearest *Ambrosia* neighbours led to a significant increase in the size of *Ambrosia* plants over a 4-year period, while control plants with neighbours present

did not increase in size (Schenk & Mahall 2002). Negative interactions between *Ambrosia* semi-shrubs are probably due to root interactions, because canopies of neighbours typically do not overlap. *Ambrosia* roots extend laterally for about 1–1.6 m from the stem (Cannon 1913; Wallace & Romney 1972), a typical distance for semi-shrubs (Schenk & Jackson 2002), and this coincides exactly with the scale of spatial segregation found for this species on sand (< 1.6 m, Fig. 3A). *Ambrosia* roots have been found to possess a self/non-self recognition mechanism (Mahall & Callaway 1991, 1992, 1996) which may lead to the spatial segregation of neighbouring root systems, and thus to the creation of root territories (Schenk *et al.* 1999). Root interactions may also be responsible for the strongly negative effects that mature *Ambrosia* have on their seedlings (Vasek 1979/80; Prose *et al.* 1987; Hunter 1989; Miriti *et al.* 1998; Schenk & Mahall 2002).

Although strongly negative effects of conspecific neighbours on canopy sizes of *Ambrosia* were found on both substrates (Table 5), spatial segregation of *Ambrosia* was only observed on sand. *Ambrosia* plants had similar densities on both substrates (Table 1), but were larger and had the highest biomass density of all woody species on sand (Table 1). This may explain why they were more affected by intraspecific than interspecific competition (Table 5 and experimental results in Schenk & Mahall (2002)). Larger woody plants also tend to have larger lateral root spreads (Schenk & Jackson 2002), another factor that may contribute to the spatial segregation on sand. Moreover, *Ambrosia* plants may compete not only with their conspecific neighbours for soil resources, but also with the many annuals that are associated with those neighbours (Fig. 2).

INTERSPECIFIC SPATIAL PATTERNS

The spatial distribution of *Ambrosia* relative to other woody species appeared to be independent of habitat characteristics. *Ambrosia* semi-shrubs everywhere were spatially segregated from the much larger *Larrea* shrubs at scales of 0–2.6 m. Such spatial segregation of *Ambrosia* from *Larrea* has been found elsewhere (Phillips & MacMahon 1981; Mahall 1998). The zone of segregation coincides with the lateral root spreads of *Larrea* shrubs, which average around 3 m (Brisson & Reynolds 1994; Cannon 1911; Singh 1964; Yeaton *et al.* 1977; Gile *et al.* 1998). Below-ground interference between *Larrea* and *Ambrosia* has been documented (Fonteyn & Mahall 1978, 1981), and living *Larrea* roots were found to inhibit growth of *Ambrosia* roots by exuding unidentified allelopathic substances (Mahall & Callaway 1992; Schenk *et al.* 1999). It appears that negative interactions with *Larrea* roots cause the co-dominant semi-shrubs to cluster outside the c. 3-m interaction radius of *Larrea* shrubs (Fonteyn & Mahall 1978, 1981; Phillips & MacMahon 1981; Schlesinger & Jones 1984; Mahall 1998). If the species

that predominantly determines community structure can be viewed as the superior competitor, then these observations lend support to the prediction of Lehman & Tilman (1997) that inferior competitors tend to be spatially more aggregated than superior competitors.

Net-positive effects of *Ambrosia* on *Acamptopappus* may explain the observed aggregation between these two semi-shrub species. In experimental studies, *Acamptopappus* growing close to *Ambrosia* neighbours at times had higher predawn xylem pressure potentials than *Acamptopappus* which had the *Ambrosia* neighbour removed (Schenk & Mahall 2002), possibly because *Acamptopappus* benefited from water leaking out from *Ambrosia* roots at night (Yoder & Nowak 1999). Interactions between these two species appear to be complex and depend in part on which species is on the more shaded northern side of the other (Schenk & Mahall 2002).

Conclusions

Overall, this study suggests that abiotic conditions can strongly influence the spatial organization of plant communities. This has been found previously in comparisons of communities under different climatic conditions (Barbour 1973; Padien & Lajtha 1992; Callaway 1998), but our findings suggest that relatively subtle differences in edaphic characteristics may also cause differences in the spatial structure of immediately adjacent plant communities. The observed temporal and spatial variability of plant interactions and spatial patterns in these desert communities suggests that the balance between positive and negative interactions may easily shift in response to environmental variability in space and time (Casper 1996; Tielbörger & Kadmon 1997, 2000; Schenk 1998). In resource-poor environments, interactions between plants can have large effects on growth and survival, because the base levels of many resources are so low that relatively small additions or removals can have disproportionately large effects on plant growth and survival. It is therefore not surprising that habitats of low productivity appear to be the ones where both the most intense net positive interactions as well as the most intense net negative interactions are to be found (Goldberg *et al.* 1999).

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Supplementary material

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/JEC/JEC782/JEC782sm.htm>

Appendix Methods used to estimate plant biomass of annuals and semi-shrubs per area.

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