

TWENTY YEARS OF CHANGES IN SPATIAL ASSOCIATION AND COMMUNITY STRUCTURE AMONG DESERT PERENNIALS

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Abstract. I present results from analyses of 20 years of spatiotemporal dynamics in a desert perennial community. Plants were identified and mapped in a 1-ha permanent plot in Joshua Tree National Park (California, USA) in 1984. Plant size, mortality, and new seedlings were censused every five years through 2004. Two species, *Ambrosia dumosa* and *Tetradlea hallii*, were dominant based on their relative abundance and ubiquitous distributions. Spatial analysis for distance indices (SADIE) identified regions of significantly high (patches) or low (gaps) densities.

I used SADIE to test for (1) transience in the distribution of patches and gaps within species over time and (2) changes in juvenile–adult associations with conspecific adults and adults of the two dominant species over time. Plant performance was quantified in patches and gaps to determine plant responsiveness to local spatial associations.

Species identity was found to influence associations between juveniles and adults. Juveniles of all species showed significant positive spatial associations with the dominant *A. dumosa* but not with *T. hallii*. The broad distribution of *A. dumosa* may increase the spatial extent of non-dominant species that are facilitated by this dominant.

The spatial location of patches and gaps was generally consistent over time for adults but not juveniles. Observed variability in the locations of juvenile patches and gaps suggested that suitable locations for establishment were broad relative to occupied regions of the habitat, and that conditions for seed germination were independent of conditions for seedling survival.

A dramatic change in spatial distributions and associations within and between species occurred after a major drought that influenced data from the final census. Positive associations between juveniles and adults of all species were found independent of previous associations and most species distributions contracted to areas that were previously characterized by low density.

By linking performance to spatial distribution, results from this study offer a spatial context for plant–plant interactions within and among species. Community composition could be influenced both by individual species tolerances of abiotic conditions and by the competitive or facilitative interactions individuals exert over neighbors.

Key words: *Ambrosia dumosa*; community dynamics; desert perennials; Joshua Tree National Park, California; SADIE; spatial distribution; species association; *Tetradlea hallii*.

INTRODUCTION

As plants are sessile organisms, their performance is strongly influenced by local biotic and abiotic conditions that over time generate patterns in their spatial distributions (Miriti et al. 1998, Dovciak et al. 2003, Maestre et al. 2005). Growth, fecundity, and survival of plants reflect physiological responses to conditions in their immediate surroundings. However, the local conditions that influence plant performance and spatial distribution are not constant in space and time. Community composition is determined by combinations of positive and negative interactions among plants (Callaway and Walker 1997) and coexistence is mediated

by spatial and temporal variations in environmental conditions (Barot 2004). Spatial distributions, then, reflect the net result of positive and negative interactions between neighbors in response to local abiotic conditions that may vary in intensity through space and time.

Because the processes that generate spatial distributions are dynamic, spatial distributions themselves should be dynamic. In general, the strength of inferences of process from pattern is more robust with sequential observations and when spatial patterns are correlated with structuring forces. Forces such as species' responses to disturbance (Wiegand et al. 1998), demographic constraints (Miriti et al. 1998, 2001, Toft and Frazer 2003), and abiotic gradients (McAuliffe 1994, Malkinson et al. 2003, Schenk et al. 2003) have provided valuable insight into the processes generating broad-scale spatial distributions within or among species. However, the most intense interactions among plants

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occur within local neighborhoods (Pacala and Silander 1990, Tilman 1994). Spatial approaches that detect pattern at local scales are more likely to capture small scale changes in pattern.

Precipitation and neighbors are two variables that may influence spatial associations in arid systems. Experimental and spatial studies show that soil moisture and neighbors mediate competitive and facilitative interactions that are correlated with spatial segregation or aggregation (Miriti et al. 1998, Holzapfel and Mahall 1999, Goldberg et al. 2001, Malkinson et al. 2003, Toft and Fraizer 2003). In deserts, precipitation is highly variable in time and space, and regulates seedling establishment (Went 1949, Beatley 1974, Schwinning et al. 2004 and references therein) and mortality (Miriti et al. 2007). Neighbor identity is particularly important in arid communities because facilitated establishment from nurse plants is common and may strongly influence species' persistence (McAuliffe 1988, Tewksbury and Lloyd 2001). In communities where dominance is high, the likelihood of neighboring a dominant is biased. Consequently, the predominant plant interactions that influence relative abundance are likely to be biased towards the competitive or facilitative ability of the dominant species and are expected to influence spatial distributions within and among species.

I present analyses of spatial associations within and between members of an arid perennial community that have been mapped and monitored for 20 years. During this 20-year interval, the region has undergone two major drought episodes and several El Niño events (Cook et al. 2004). Two species, *Ambrosia dumosa* (Gray) Payne (Asteraceae) and *Tetradococcus hallii* (Asteraceae), are dominant at this site based on their abundance and ubiquitous spatial distributions. *A. dumosa* has been recognized as a nurse plant in this and other deserts (McAuliffe 1988, Holzapfel and Mahall 1999, Miriti 1999); the facilitative ability of *T. hallii* has not been established. Previous studies in this system identified significant spatial structure within juveniles and adults of common species (Howe and Wright 1986, Wright and Howe 1987, Miriti et al. 1998). Patterns of establishment, growth, and mortality for common species including the dominant *A. dumosa* suggest plant performance is responsive to local spatial pattern and neighbor status (Miriti et al. 1998, 2001, Miriti 2006). Therefore, the study system is well suited to study of the effects of temporal variation in habitat quality and neighbor identity on spatial associations.

To determine the influence of dominant species and temporal variation in habitat quality on performance and persistence within this community, I conduct analyses that link spatial pattern with measures of plant performance. To observe changes in local pattern over time, I conduct spatial analyses that isolate individual regions of high and low density of focal species for each census interval. I then measure changes in plant performance within each high- or low-density region to

quantify if there is a consistent relationship between pattern and performance. To interpret pattern, I assume (1) changes in spatial distributions result from plant establishment, growth, and mortality and (2) changes in demographic performance reflect the quality of local conditions. Therefore, local regions of significant high or low density may decrease or disappear over time due to shrinkage or mortality of occupants, or appear or increase in space due to increased juvenile establishment, increases in plant size or both. Because plant growth and mortality are dependent on plant size, I conduct separate analyses for juvenile and adult size classes. The expectations are (1) growth or survival should be maximized within favorable locations, (2) growth or survival should be maximized where favorable associations occur, and (3) conversion from high to low density or from low to high density reflects changes in local habitat quality.

METHODS

Study system and species

The study site is a mapped 1-ha plot of predominantly shrub species located near Cottonwood Springs within Joshua Tree National Park, California, USA, approximately 10 km from the interface of the Colorado Desert with the Mojave Desert. The data here presented are from plants mapped in 1984 and censused at five-year intervals through 2004 with the exception of a one-year census in 2000. This hectare is located on an erosion-derived formation known as a bajada, of 1–4% slope near the base of the Eagle Mountains. Prior to study initiation, this site enjoyed 44 years without anthropogenic disturbance; grazing has not occurred near Cottonwood Springs since 1940 (Greene 1983), prior to which time, light grazing occurred from 1916 to 1917 and again in the late 1930s.

Only species with all life-history stages present at the study site are included in this study. Most notably, the creosote bush, *Larrea tridentata*, is not included in these analyses. Although conspicuous, *L. tridentata* has not produced seedlings and is represented by very few juveniles (<20) over 20 years. The remainder of the species not included is represented by very small population sizes. Nomenclature follows Munz (1974). Focal species are *A. dumosa* (Asteraceae), *Tetradococcus hallii* (Euphorbiaceae), *Eriogonum fasciculatum* (Polygonaceae), *Opuntia ramosissima* (Cactaceae), *Sphaeralcea ambigua* (Malvaceae), and *Simmondsia chinensis* (Buxaceae).

Spatial analyses

The mapped *x*, *y* locations of plants were used to establish count data required for the spatial analyses. Count data were obtained by gridding the 100 × 100 m sample area into 400 5 × 5 m² quadrats and counting the number of target individuals in each quadrat.

Spatial distributions for each census were analyzed using spatial analysis by distance indices (SADIE; Perry

1995, Perry et al. 1999). These analyses use spatially referenced counts to identify clusters of locally high density (patches) or low density (gaps). The analyses use quadrat counts to generate the null hypothesis that counts are randomly distributed in the study arena. The parameter D is the minimum distance required to reorganize the observed counts within the study arena to obtain a uniform distribution. A mean value of D , D_m is obtained by averaging D from multiple iterations in which observed counts are randomly distributed in the sample area. The ratio between D and D_m is used to calculate an index of aggregation, I_a , which when greater than or equal to unity identifies significant clusters of patches or gaps throughout the study area (Perry et al. 1999, Winder et al. 2001).

Local cluster indices, v_i representing patches and v_j representing gaps are assigned to each $5 \times 5 \text{ m}^2$ quadrat to describe local pattern; v_i and v_j are determined using data obtained during the redistribution of points described above. Details for calculating v_i and v_j can be found in Perry et al. (1999). The expectation of v_i is 1 and the expectation of v_j is -1 . From Perry et al. (1999), values of $v_i > 1.5$ and $v_j < -1.5$ indicate a significant patch or gap, respectively. Cluster indices can be mapped and contoured, producing red–blue maps that show the precise locations and topographies of gaps, which are shaded in blue, and patches, which are shaded in red. Not only is significant pattern detected, but individual regions of significant pattern are specifically identified in space, providing an opportunity to identify and measure spatiotemporal cluster stability, habitat partitioning by species, and spatial associations within and between species.

In addition to determining the spatial distribution of focal populations, I also analyzed spatial associations, which describe the spatial relationship between two populations, such as juveniles and adults within a species, and are denoted by the local association index χ_k . This index is determined by comparing the value of local cluster indices of two populations at the k th quadrat (Winder et al. 2001). Specifically, z_{k1} refers to the value of the cluster index for population 1 at the k th quadrat, and z_{k2} refers to the cluster index value of the k th quadrat for population 2. If q refers to the mean of cluster indices for a given population, then for n quadrats,

$$\chi_k = n(z_{k1} - q_1)(z_{k2} - q_2) / [\sum_k (z_{k1} - q_1)^2 \sum_k (z_{k2} - q_2)^2]^{0.5}.$$

By referencing population-specific cluster indices, bias related to differences in overall population density is avoided. Positive associations ($\chi_k > 0$) occur when local cluster indices, v_i or v_j , have the same sign; negative associations ($\chi_k < 0$) occur when they have different signs. Overall association between two populations, X , is the mean of the local χ_k . Significance of X is determined by random reassignment of the local cluster indices for each population and with allowance for small scale autocorrelation of v_i and v_j for each population

(Dutilleul 1993, Winder et al. 2001). As with local cluster indices, local association indices can be contoured to explicitly map regions of significant association.

I used association analysis to address two distinct questions. Association analysis was first used to test the integrity of spatial distributions over time, and second to test the spatial association between juveniles and (1) conspecific adults and (2) adults of each of the two dominant species.

The first test quantified how well the spatial distribution of a population at one point in time predicted the distribution of that same population in the future. If the spatial distribution of a population is static, the expectation of X is unity because local cluster indices will have the same value over time. If distributions constantly shift such that the value of cluster indices at time t are not observed at $t + x$, the expectation of X is zero; if the value of cluster indices change from positive to negative or vice versa over time, X is negative. The second use of association analyses addressed the potential for facilitation or competition between juveniles and conspecific adults or adults of the dominant species *A. dumosa* and *T. hallii*. Significant positive associations between juveniles and target adult species suggested facilitation or an affinity for abiotic conditions positively associated with target adult canopies; significant negative associations suggested competition or lack of tolerance of abiotic conditions positively associated with target adult canopies.

Plant performance

To strengthen inferences of the biological significance of pattern, I used plant size as an indicator of plant performance. For each census, mean plant volume of juveniles and adults in each $5 \times 5 \text{ m}$ quadrat was calculated. Plants were categorized as juvenile or adult based on the volume at which a critical proportion of plants within a species presents reproductive structures (see Wright and Howe 1987). To determine differences in performance in response to spatial distribution, I measured (1) juvenile and adult volume in response to local dispersion, as determined by significant cluster indices and (2) juvenile volume in response to associations with both conspecific adults and adults of the dominants *A. dumosa* and *T. hallii*.

For the first analysis, contour maps of clusters from each census were digitized to determine the boundary x – y coordinates of individual gaps and patches. These coordinates were then cross-referenced with the original census data to identify each plant occurring in the individual clusters and to estimate the mean volume of individual plants in each cluster. By averaging over plant volume within each patch or gap, each mean volume/cluster type represents a measure that can reasonably be regarded as independent (J. Perry, *personal communication*). For each census, the significance of differences between the mean volumes of plants located in patches

compared to gaps was determined using two-tailed t tests.

For the second analysis, I used regression analyses to test the dependence of juvenile volume on local associations with adults. These analyses were constrained to those species that showed significant associations with conspecific adults and adults of either dominant species. Local density frequently limits growth and may generate a ceiling or floor in the size distribution of plants in response to a variable that influences density (Crowell and Boerner 1988, Thomson et al. 1996, Lessin et al. 2001, Cade and Noon 2003). In such cases, the mean response to an independent variable is an inadequate measure of ecological dynamics. Mean plant size is a potentially misleading index of the impact of associations between juveniles and adults because skewed distributions give unrepresentative means. For example, if the positive associations reflect high rates of seed germination, the abundance of small seedlings will bias average juvenile size downward even if there are many large juveniles. For this reason, I used boundary regressions, which conduct regression analyses on the edges of response distributions (Lessin et al. 2001) to evaluate influences of local associations on juvenile performance. The values of association indices were grouped to ensure that a minimum and maximum juvenile volume was obtained for all given ranges of values of the association index. Separate regressions were conducted for positive and negative associations, and for upper and lower edges. The lower edge of the response distribution of juvenile size to the value of local association was interpreted to reflect the frequency of seedling establishment and limitations on growth, and the upper edge was interpreted to reflect limitations on reaching reproductive size.

RESULTS

Spatial analyses

The sign and magnitude of the overall index of aggregation, I_a and the mean local cluster indices (v_i and v_j) measured the extent of spatial structure within species. Red–blue maps revealed patches and gaps for each species (Fig. 1). Significant spatial structure, indicated by the significance of I_a (Table 1), was consistently observed for juveniles and adults of *A. dumosa* and *E. fasciculatum* for all censuses and for *T. hallii* adults from 1994 forward.

When association analyses were used to test the spatial stability of patches and gaps over time, the spatial distribution of patches and gaps was generally

consistent over time for adults of all species except *S. ambigua*, and for all censuses until 2004 ($P < 0.01$, Table 2). Juvenile distributions were also consistent over time, but the magnitudes of the associations were not as strong as those of adults (Table 2). Although not statistically significant, the distribution of adult patches and gaps in 2004 was largely independent of previous adult distributions. In fact, all species showed contracted distributions from the 2004 census (Fig. 2) with large clusters of negative associations (Table 2) indicating that patches from previous censuses were frequently identified as gaps in 2004.

When association analyses were used to compare the distribution of juveniles relative to conspecific adults, and *A. dumosa* and *T. hallii* adults, results showed that associations were sensitive to adult identity (Table 3). Overall associations, X , were significant and positive for intraspecific comparisons over all censuses of *A. dumosa* and *E. fasciculatum*. For interspecific associations, X was consistently significant and positive between adults of the dominant *A. dumosa* and juveniles of *E. fasciculatum*, *S. chinensis*, and *S. ambigua* except in 2004. With the exception of the 2004 data, no significant associations occurred between the dominant *T. hallii* adults and juveniles of the other focal species.

Independent of distributions in previous years, all X values were positive and highly significant in 2004. All species distributions contracted to the central region of the hectare independent of previous dispersion throughout the study site (Fig. 2). Most notably, the lower left corner of the 1-ha plot, previously a consistent area of high density for *A. dumosa*, *E. fasciculatum* and *S. ambigua* (Fig. 1) was devoid of live canopies in 2004 (Fig. 2).

Contour maps of the local associations, χ_k , between *A. dumosa* adults and juveniles of each species (Fig. 3) showed clusters of association and dissociation for all species pairs. Local associations, χ_k , were variable over time (Appendix: Figs. A1 and A2), which is likely due to patchy seedling establishment, and recruitment of large juveniles to reproductive status. Variability in the sign and magnitude of χ_k were particularly high for *S. ambigua* and *E. fasciculatum*, which suffered severe losses of juveniles and reduced establishment of seedlings over the 20-year interval. By 2004, no juveniles of *E. fasciculatum* or any individual of *S. ambigua* were observed.

It is important to recognize that positive associations between populations occur in clusters that are mutually favorable or mutually unfavorable for both members of

FIG. 1. Contour-post maps of spatial analysis for distance indices (SADIE) red–blue analysis of quadrat counts for 1994 data. Adults are shown in the top two rows and juveniles in the bottom two rows. Shaded areas delineate regions of significant pattern: local cluster index values (v_i or v_j) greater than 1.5 indicate patches (red); values less than -1.5 indicate gaps (blue). Solid circles identify 5×5 m quadrats in which $|v_i, v_j| > 1.5$. Similarly, open circles identify 5×5 m quadrats with $1 < v_i < 1.5$ (red) or with $-1 > v_j > -1.5$ (blue). Species are *Ambrosia dumosa*, *Eriogonum fasciculatum*, *Opuntia ramosissima*, *Sphaeralcea ambigua*, *Simmondsia chinensis*, and *Tetracoccus hallii*.

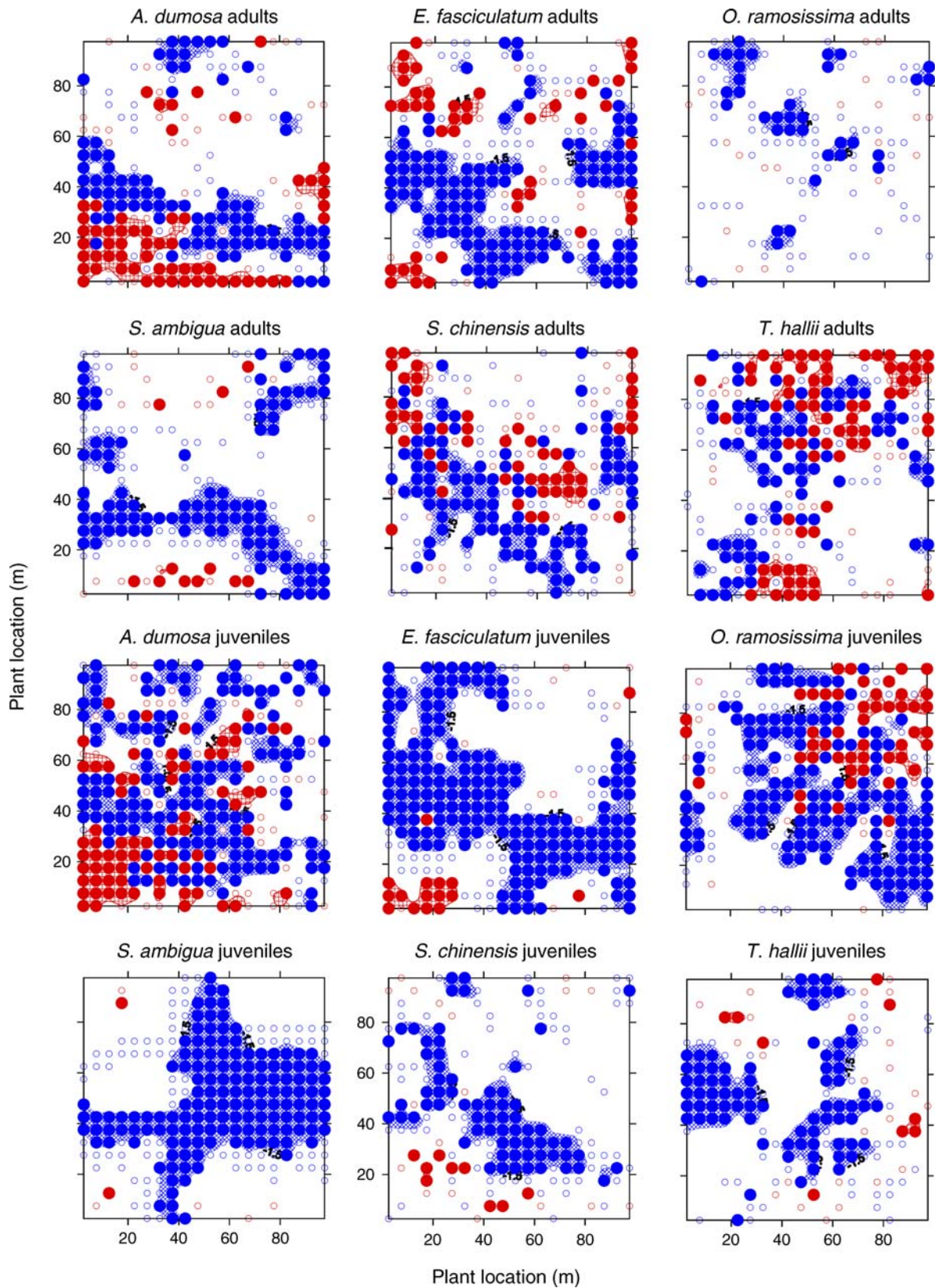


TABLE 1. Summary statistics of spatial analysis for distance indices (SADIE) analyses of focal species.

Species and year	Adults			Juveniles		
	I_a	v_j	v_i	I_a	v_j	v_i
<i>Ambrosia dumosa</i>						
1984	1.503	−1.491	1.371*	1.604	−1.535	1.434
1989	1.506	−1.480	1.363*	1.624	−1.590	1.448
1994	1.633	−1.511	1.477	2.256	−2.268	1.966
1999	1.581	−1.523	1.151	3.165	−3.133	2.626
2000	1.595	−1.521	1.512	2.639	−2.514	2.262
2004	1.787	−1.707	1.824	1.860	−1.881	1.854
<i>Tetracoccus hallii</i>						
1984	1.214	−1.215	1.215	1.222	−1.211	1.239
1989	1.196	−1.192	1.200	1.316*	−1.301*	1.326*
1994	1.457	−1.448	1.474	1.128	−1.116	1.141
1999	1.362*	−1.343*	1.369*	1.116	−1.106	1.117
2000	1.361*	−1.347*	1.340*	1.150	−1.141	1.131
2004	1.651	−1.669	1.538	1.295	−1.287	1.384*
<i>Eriogonum fasciculatum</i>						
1984	1.480	−1.476	1.525	1.641	−1.632	1.648
1989	1.546	−1.542	1.629	1.496	−1.490	1.903
1994	1.482	−1.472	1.595	1.750	−1.748	1.675
1999	1.538	−1.527	1.713	1.588	−1.582	1.530
2000	1.420*	−1.415*	1.510	1.618	−1.611	1.740
2004	1.281	−1.283	1.263			
<i>Opuntia ramosissima</i>						
1984	0.893	−0.895	0.876	1.178	−1.174	1.179
1989	0.893	−0.895	0.875	1.810	−1.798	1.703
1994	0.887	−0.889	0.864	1.856	−1.858	1.825
1999	0.908	−0.909	0.900	1.482	−1.487	1.373
2000	0.912	−0.916	0.904	1.565	−1.562	1.449
2004	1.214	−1.220	1.222	1.274	−1.274	1.268
<i>Simmondsia chinensis</i>						
1984	1.254	−1.245	1.212	1.089	−1.085	1.059
1989	1.253	−1.245	1.210	1.116	−1.110	1.105
1994	1.511	−1.500	1.468	1.083	−1.079	1.073
1999	1.444	−1.435	1.418	1.074	−1.074	1.018
2000	1.372*	−1.365*	1.339*	1.091	−1.088	1.037
2004	1.499	−1.503	1.520	1.069	−1.066	1.032
<i>Sphaeralcea ambigua</i>						
1984	1.245	−1.239	1.265*	1.072	−1.073	1.023
1989	1.983	−1.998	2.014	1.212	−1.207	1.135
1994	1.130	−1.131	1.223	1.272	−1.285	1.233
1999	1.072	−1.070	1.081	1.877	−1.887	1.912
2000	1.119	−1.120	1.110	1.379*	−1.380*	1.321*

Notes: I_a , the index of aggregation, reflects the magnitude of overall spatial structure presented by a focal population; v_i and v_j designate the mean value of patch and gap indices, respectively. Indices with $P < 0.01$ are indicated in bold. An asterisk indicates $0.01 < P < 0.05$.

a species pair. Although all interspecific comparisons exhibited both types of positive associations, mutually favorable contours were most apparent for the association between *A. dumosa* juveniles and adults and *E. fasciculatum* and *S. ambigua* juveniles and *A. dumosa* adults. Contours of negative association most consistently contained adults and not juveniles, suggesting unfavorable establishment sites or juvenile exclusion.

Comparing overlays between intraspecific associations and associations with *A. dumosa* adults identified regions where species overlap and regions where *A. dumosa* potentially expanded the distribution of secondary species. These occurred for *O. ramosissima*, *T. hallii*, *S. chinensis*, and *S. ambigua* but not *E. fasciculatum*,

which as stated above shared areas of high density with *A. dumosa*.

Plant performance

Cluster analyses.—Because cluster and association indices are based on count data, contrasts between gaps and patches reflect variation in local densities of each species and their dispersion throughout the study site. For broadly dispersed species (*A. dumosa* and *T. hallii*), gaps contain plants, but at low densities, while for the remaining species gaps do not contain plants. *A. dumosa* was the only species that presented a sufficient number of patches and gaps containing plants for all censuses to quantify the effects of local density on plant perfor-

TABLE 2. Overall associations of spatial distributions over the 20-year study period.

Species and year	Adults					Juveniles				
	1989	1994	1999	2000	2004	1989	1994	1999	2000	2004
<i>Ambrosia dumosa</i>										
1984	0.9651	0.7305	0.7414	0.7416	−0.0189†	0.5683	0.4846	0.4709	0.5749	−0.0301†
1989		0.7351	0.7360	0.7475	−0.0329†		0.5330	0.4747	0.5792	−0.0305†
1994			0.7810	0.8306	−0.0077†			0.6497	0.6421	−0.1223†
1999				0.8367	−0.0454†				0.6518	−0.1698†
2000					−0.0693†					−0.0745†
<i>Tetradococcus hallii</i>										
1984	0.5683	0.4846	0.4709	0.5749	−0.0301†	0.7916	0.5326	0.5540	0.4950	0.2229
1989		0.5330	0.4747	0.5792	−0.0305†		0.5173	0.5703	0.4940	0.2577
1994			0.6497	0.6421	−0.1223†			0.6443	0.6505	0.2387
1999				0.6518	−0.1698†				0.6658	0.2472
2000					−0.0745†					0.1772
<i>Eriogonum fasciculatum</i>										
1984	0.9296	0.8042	0.7937	0.8161	0.2106*	0.6295	0.0978†	0.2546	0.3248	
1989		0.7959	0.8089	0.8050	0.1914*		0.1992	0.2855	0.3051	
1994			0.9077	0.9064	0.2618			0.5105	0.5933	
1999				0.9106	0.2080*				0.6692	
2000					0.2012*					
<i>Opuntia ramosissima</i>										
1984	0.9999	0.8194	0.6715	0.6803	0.3731	0.4109	0.2936	0.1830	0.2149	0.0456†
1989		0.8195	0.6722	0.6799	0.3717		0.6006	0.4458	0.5022	0.1677
1994			0.8242	0.8379	0.3217			0.7155	0.7644	0.1137†
1999				0.7878	0.3012				0.8155	0.0837†
2000					0.3147					0.0588†
<i>Simmondsia chinensis</i>										
1984	0.9999	0.8579	0.8194	0.8547	0.3991	0.7603	0.6997	0.5917	0.6802	−0.0219†
1989		0.8578	0.8199	0.8550	0.3997		0.6945	0.6393	0.7043	−0.0084†
1994			0.8668	0.8797	0.3890			0.7360	0.7855	0.0546†
1999				0.8513	0.4592				0.8029	0.0517†
2000					0.4115					0.0151†
<i>Sphaeralcea ambigua</i>										
1984	−0.0006†	0.3743	0.4298	0.4637		0.5679	0.0553†	−0.1090†	−0.0180†	
1989		0.1112*	0.1459	0.0244†			0.1147†	0.0295†	0.1536*	
1994			0.4799	0.6312				0.1008	−0.1622†	
1999				0.5040					0.3670	

Notes: Association values range from −1 to 1. All associations except those that are marked were significant at $P < 0.01$. Positive values indicate the degree of similarity of the spatial distribution of plants from the census date shown on the left to the census date shown above the column. Negative values indicate the degree of dissimilarity.

* $0.01 < P < 0.05$.

† Not significant.

mance. The number of gaps and patches varied with census year. Differences in mean volume of plants in patches and clusters revealed that *A. dumosa* adults in gaps were larger than those in patches for 1989 and 1994 (1989, $t = 2.61$, $P = 0.032$; 1994, $t = 3.18$, $P = 0.032$). There were no significant differences in adult plant size between cluster types for the other censuses. Juvenile size showed significant temporal variation ($t = -2.30$, $P = 0.02$), but for any individual census averages of the two cluster types were similar.

Association analyses.—Effects on plant size of intra-specific association between juveniles and adults of *A. dumosa*, *E. fasciculatum*, *S. chinensis*, and *S. ambigua*, and interspecific associations between juveniles of these species and adults of *A. dumosa* were assessed with boundary regressions of plant volume on the local association index, χ_k (Table 3). Although the most consistent effects were seen at the lower boundary,

juvenile responses to association with conspecific adults or *A. dumosa* adults were distinct.

For *A. dumosa*, the upper boundary was flat indicating that juveniles reached reproductive size at all association values and suggesting that growth of large juveniles was not limited by adult association. In contrast, the size and frequency of smaller juveniles varied with the sign and intensity of the association and with census year. The absence of small plants with increasing absolute magnitude of χ_k suggests that growth or survival of seedlings is limited by both extreme aggregation and isolation. Regressions of the lower boundary often had negative slopes for negative associations and positive slopes for positive associations (Table 4). This result suggests a benefit for juveniles in close proximity to conspecific adults or that local associations between adults and juveniles may reflect local abiotic conditions. Although R^2 values were high

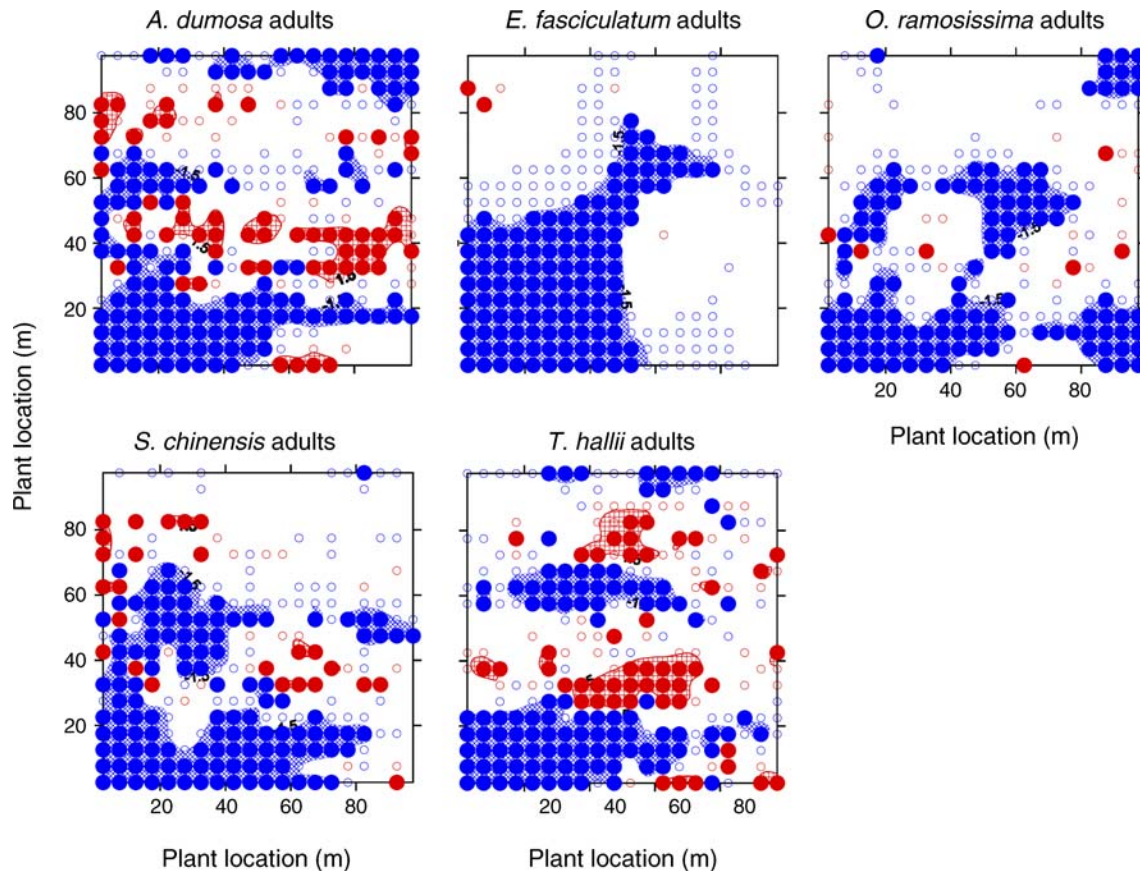


FIG. 2. Contour-post maps of spatial analysis for distance indices (SADIE) red-blue analysis for 2004 data (adults only). All species experienced high mortality and showed contracted distribution at the study site. See Fig. 1 for symbol descriptions and species names.

TABLE 3. Overall associations between adults and juveniles of species pairs examined.

Adult species	Juvenile species	Overall association (χ^2)					
		1984	1989	1994	1999	2000	2004
AD	EF	0.1674*	0.1359*	0.2391	0.1941	0.2093	†
AD	OR	0.0713	0.2071	0.1270	0.1794	0.1584	0.3591
AD	SA	0.4726	0.2646	0.1071	0.1678	0.0845	†
AD	SC	0.1893	0.2345	0.2658	0.2541	0.2343	0.4448
AD	AD	0.4726	0.4802	0.4119	0.4609	0.4548	0.6295
AD	TH	0.0752	0.1070	0.2660	0.1367*	0.2000	0.2966
TH	AD	0.0206	-0.0446	-0.0352	-0.0950	-0.0092	0.6390
TH	EF	-0.0797	0.0265	-0.0238	0.0688	-0.0717	†
TH	OR	0.1419	0.0832	0.1187	-0.0008	0.0360	0.4371
TH	SA	0.0399	-0.0657	0.0619	-0.1073	-0.0713	†
TH	SC	0.0805*	0.0276	0.0406	-0.0043	0.0199	0.3889
TH	TH	0.1243*	0.0834	0.0213	0.1085*	0.0593	0.2779
SA	SA	0.1186*	-0.0251	0.0230	0.3148	0.2151	†
SC	SC	0.1453*	0.1045*	0.2220	0.0796	0.0657	0.4698
EF	EF	0.5060	0.6399	0.2311	0.3560	0.3477	†
OR	OR	-0.0074	0.0355	0.0339	0.0305	0.0230	0.3626

Notes: Species abbreviations: AD, *Ambrosia dumosa*; TH, *Tetracoccus hallii*; SA, *Sphaeralcea ambigua*; SC, *Simmondsia chinensis*; EF, *Eriogonum fasciculatum*; OR, *Opuntia ramosissima*. Associations with $P < 0.01$ are presented in bold.

* $0.01 < P < 0.05$.

† Analysis was not conducted because one or both members of the species pair was not observed during a given census.

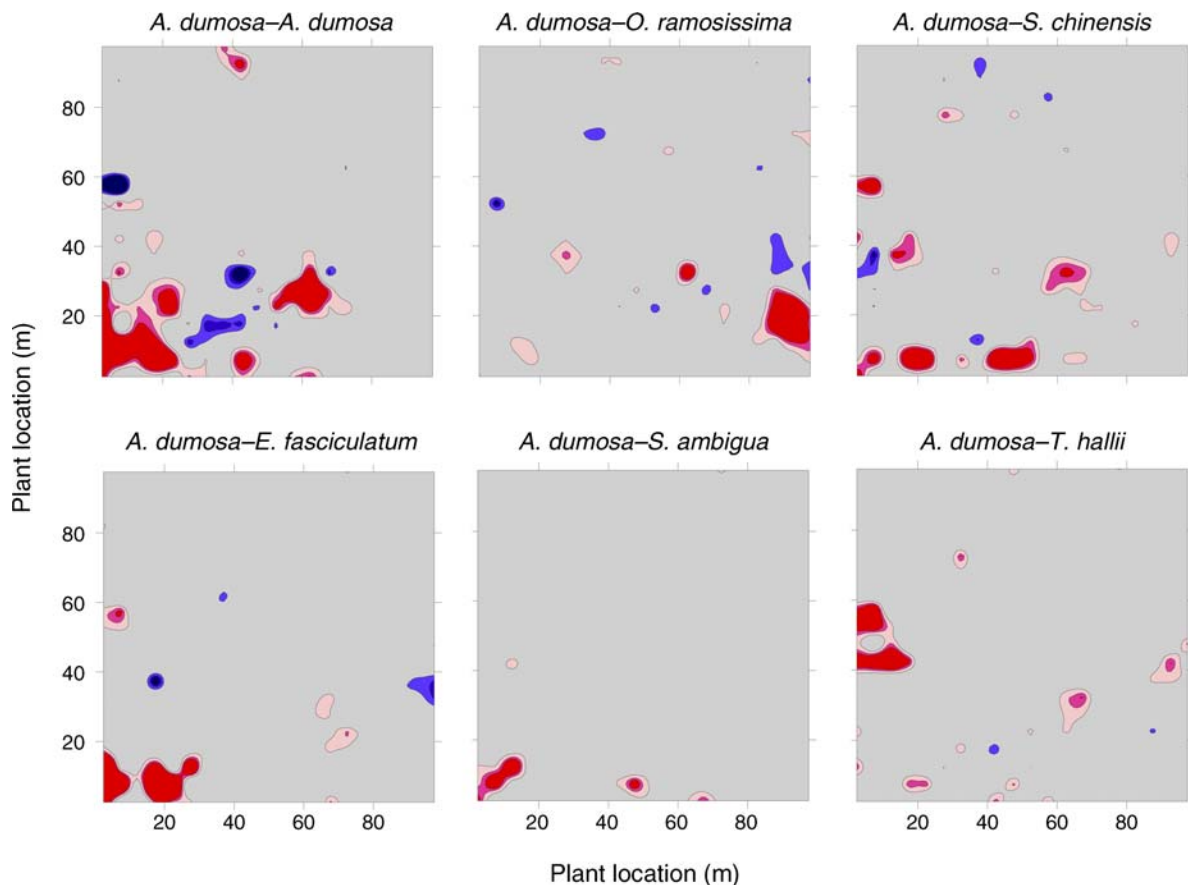


FIG. 3. Contour map of the association between counts of juveniles of each species and *Ambrosia dumosa* adults using data from the 1994 census. Red contours show positive association, and blue contours show negative association. The intensity of shading corresponds to the level of significance of the association (deep shading, $P < 0.05$; moderate shading, $0.05 < P < 0.10$; light shading, $0.10 < P < 0.25$). Species names are in the Fig. 1 legend.

for negative associations, the response to χ_k was more variable (Fig. 4), contributing to diminished significance of juvenile response. For all censuses, juvenile volume was greatest with increasing absolute value of χ_k , although differences in slope showed that the strength of this response varied more for positive χ_k .

For the non-dominant species included in the analyses, the response of juveniles to adult association varied with year and with adult species (Table 4). Juvenile responses to conspecific adults were typically distinct from responses to *A. dumosa* adults, but the significance of the responses was inconsistent even though overall associations, X , with *A. dumosa* adults were consistently positive and significant. X values may have been influenced by locations that were mutually unfavorable for both juveniles and adults. In general, the number of juveniles of non-dominant species was consistently < 100 , which reduces the ability to detect a significant response to adult associations. Nevertheless, the number of juveniles positively associated was far larger than the number of juveniles negatively associated with adults of either species.

Although inconsistent, significant associations were observed. Positive associations between juvenile *S. ambigua* and *A. dumosa* adults were significant or marginally significant for 1984 and 1989. *S. ambigua* juveniles declined consistently after 1989 and were completely absent by 2004. *A. dumosa* canopies may have provided a last refuge for juveniles of this once common species. Significant dissociations between *S. chinensis* and *A. dumosa* adults were strong and significant in 1989 and 2000 despite a greater frequency of juveniles positively associated with *A. dumosa*. Significant positive associations with conspecific adults were observed in 1984. Juvenile *S. chinensis* may be particularly sensitive to temporal variation in local habitat.

The lack of significant responses to adult association was most remarkable for *E. fasciculatum*, because no juveniles were dissociated from conspecific adults (Fig. 5). It is possible that dispersal was extremely limited for this species.

DISCUSSION

Results from this study show a species-dependent and stage-dependent relationship between spatial association

TABLE 4. Regression coefficients (r^2) and significance from boundary regression of juvenile size in response to positive and negative association with *Ambrosia dumosa* adults and conspecific adults.

Juvenile species and year	<i>Ambrosia dumosa</i> adult		Conspecific adult	
	Association	Dissociation	Association	Dissociation
<i>Ambrosia dumosa</i>				
1984	0.646**	0.752†		
1989	0.128	0.162		
1994	0.403**	0.346		
1999	0.14	0.447		
2000	0.347*	0.406†		
2004	0.535**	0.693†		
<i>Eriogonum fasciculatum</i>				
1984	0.026	‡	0.026	‡
1989	0.204	0.600†	0.159	‡
1994	0.037	0.251	0.000	‡
1999	0.068	0.581	0.052	‡
2000	0.003	0.000	0.077	‡
<i>Simmondsia chinensis</i>				
1984	0.083	0.049	0.466*	0.320
1989	0.101	0.463*	0.007	0.343
1994	0.136	0.026	0.047	0.090
1999	0.015	0.007	0.169	0.013
2000	0.103	0.534*	0.008	0.760*
2004	0.080	0.604	0.002	‡
<i>Sphaeralcea ambigua</i>				
1984	0.422†	‡	0.164	0.155
1989	0.772*	0.77*	0.084	0.670*
1994	0.108	‡	0.000	‡
1999	0.235	‡	0.061	0.942
2000	0.092	0.251	0.016	‡

* $P < 0.05$; ** $P < 0.01$; † $0.05 < P < 0.10$.

‡ Regression analysis was not performed because dissociation was not observed.

and plant performance. Juveniles of most species included in these analyses were positively associated with the dominant, *A. dumosa*, adults but were neutrally associated with the dominant, *T. hallii*, adults. With the exception of *A. dumosa*, juveniles of species that showed significant intraspecific associations (1) showed distinct size responses depending on the sign of the association and adult identity and (2) presented greater numbers of juveniles in positive associations than negative. Results also show that for most species, juvenile spatial clusters are more dynamic in space than those of adults. Plant size was variably sensitive to the relative density of neighbors within a cluster. By measuring spatial associations over time, these results provide insights into the factors that influence spatial structure within this arid plant community.

Juvenile-adult associations

It is tempting to attribute positive associations between non-dominant juveniles and *A. dumosa* adults to the commonness of *A. dumosa* within this plant community. In general, arid plant species do not possess adaptations for targeted dispersal (Ellner and Shmida 1981); seeds tend to accumulate in the vicinity of the parent plant or blow around the surface until they encounter an obstacle that prevents further dispersal. The spatial indifference of non-dominant species to *T.*

hallii adults indicates that a ubiquitous distribution is not sufficient to promote positive associations between juveniles and adults. This spatial indifference to *T. hallii* also suggests that competitive interactions between *T. hallii* and non-dominant species are not strong, and that *A. dumosa* possesses attributes that may promote juvenile establishment.

Germination and early survival of juveniles in deserts is frequently dependent on facilitation from nurse plants (Suzan et al. 1996, Raffaele and Veblen 1998, Nunez et al. 1999, Tewksbury and Lloyd 2001, Flores and Jurado 2003). *A. dumosa*'s low lying canopy is more likely to trap seeds than *T. hallii*'s more upright architecture and may contribute to the greater frequency of juveniles establishing under *A. dumosa* canopies. The ecological significance of positive associations with *A. dumosa* adults increases if seed germination, juvenile establishment or juvenile survival is enhanced as a result of the association.

Because most nondominant juveniles showed positive responses to conspecific adult canopies, the importance of *A. dumosa* may be due to its greater abundance, in addition to whatever resources specifically associated with *A. dumosa* canopies. Local distributions are likely expanded when juveniles are unambiguously positively associated with *A. dumosa*, but not with a conspecific adult as occurred for *O. ramosissima*, *T. hallii*, *S. chinensis*,

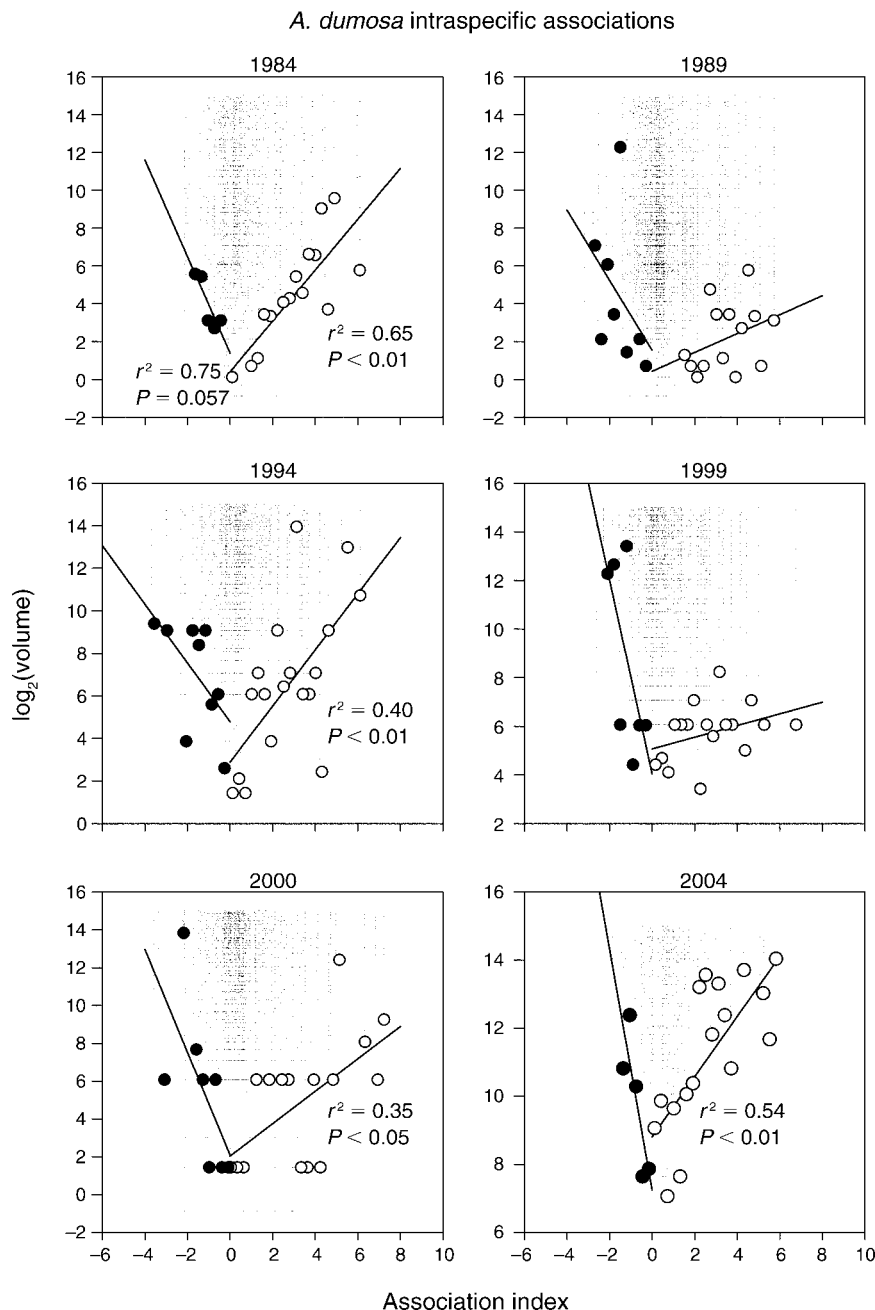


FIG. 4. Scatter plot diagrams of log-transformed juvenile volume (originally measured in cm^3) in response to local association index (χ_k , which reflects the synchrony of spatial distributions between two populations [see *Methods*]) for *Ambrosia dumosa* adult–juvenile associations. Regression lines show the response of the lower boundary, which is indicated with open circles for positive χ_k and solid circles for negative χ_k ; χ_k was binned to eliminate values without juvenile representation. The absence of small plants with increasing absolute magnitude of χ_k suggests that establishment or survival of seedlings is limited by both extreme aggregation and isolation. Plants reach adult size at all intensities of association. Note different scale numbers on y-axes.

and *S. ambigua*. This spatial response is potentially important for species in which juveniles rarely establish without close association with an adult canopy (e.g., *E. fasciculatum* and *S. ambigua* [Miriti et al. 1998]) and when juvenile performance is improved by the association.

If adult *A. dumosa* canopies represent safe sites, reliability of these adult distributions may be an important regulator of community dynamics. Although positive juvenile–adult associations are common for *A. dumosa*, it is also common to find juveniles thriving far

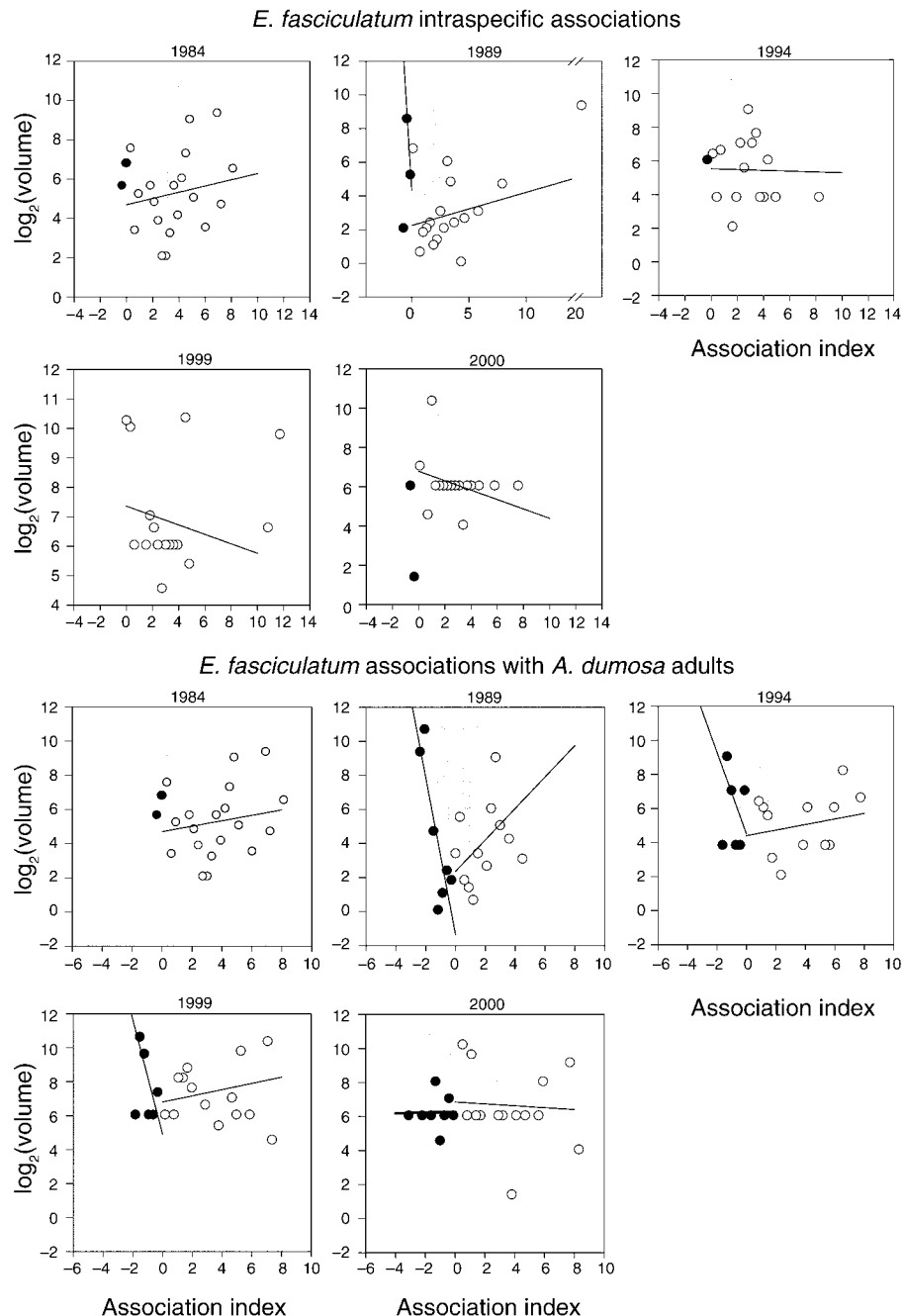


FIG. 5. Scatter plot diagrams of juvenile volume in response to local association index (χ_k , which reflects the synchrony of spatial distributions between two populations [see *Methods*]) for juvenile associations with *Ambrosia dumosa* adults and with conspecific adults for *Eriogonum fasciculatum*. Regression lines show the response of the lower boundary, which is indicated with open circles for positive χ_k and solid circles for negative χ_k ; χ_k was binned to eliminate values without juvenile representation. The relatively flat response of maximum juvenile volume with χ_k suggests that recruitment to adult size is not influenced by association value. However, the number of juveniles with positive associations exceeds those with negative associations, suggesting limited dispersal or facilitative interactions. Distinct slopes for intra- and interspecific associations show species-specific responses of juveniles.

from adults. Despite prevalent aggregation in *A. dumosa*, isolated individuals are common, and in fact, drive population dynamics (Miriti et al. 2001). This ability to recruit adults in isolated and nursed conditions

may reflect a broad tolerance of habitat conditions and may ensure the broad spatial extent of this dominant. Long-term monitoring of individual plants as a function of initial adult association will help to clarify popula-

tion- and community-level significance of associations between nondominant juveniles and adult *A. dumosa*.

Spatial distributions over time

Typically, higher mortality rates during early life history stages (Pfister 1998) associated with lower resistance to variation in abiotic and biotic conditions lead to considerable variation in juvenile distributions. Desert plant communities are, furthermore, often subjected to harsh abiotic conditions that generate slow growth rates and contribute to precarious juvenile development. Juvenile clusters in this study also vary in location over time whereas adult clusters are, for the most part, stable. Only the relatively short-lived species (~5–15 years [Miriti 1999]), *S. ambigua*, had variable adult distributions. Long potential life spans of desert shrubs (e.g., Bowers et al. 1995, Miriti 1999) combined with low mortality of adults contribute to the apparently static spatial pattern exhibited over five-year windows by most adults in this study.

One striking finding of this study is the dramatic shift in spatial distributions that accompanied a drought-induced mortality episode observed during the 2004 census (Miriti et al. 2007). This mortality appears to be spatially nonrandom and may be density dependent. The region of the study site that consistently contained high densities of the most numerous species did not contain live canopies of either adults or juveniles of any of the focal species after the extensive drought that plagued large portions of the Southwest including southern California from 2000 to 2003 (Cook et al. 2004).

Although negative associations between locations of patches and gaps during previous censuses and those in 2004 are not significant, the locations of patches and gaps during previous censuses does not strongly predict those in 2004. In other words, there was a shift in the distribution of high- and low-density clusters from previous censuses in 2004. Mean size of the common *A. dumosa* adults is consistently smaller in the typically dense lower left corner of the study site than in less dense areas for all censuses preceding 2004, and plants that suffered mortality in 2004 experienced greater negative growth during previous censuses (Miriti et al. 2007).

Large recruitment events are expected to follow episodes of heavy adult mortality if these episodes coincide with favorable rainfall (Wiegand et al. 1995). This post-drought recruitment should not be spatially independent, but should occur in safe sites, which may be associated with locations of adult mortality if standing dead canopies protect seedlings from herbivory without later competition for soil moisture as seedlings grow or habitat conditions change (e.g., Holzapfel and Mahall 1999). Continued monitoring of the study site will determine the persistence of the spatial effects here documented.

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APPENDIX

Figures showing changes in juvenile–adult associations over time (*Ecological Archives* E088-074-A1).