

Pattern and mortality in Colorado Desert plants

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Summary. We tested for intraspecific interference among Colorado Desert shrubs using an integrated analysis of spatial pattern and juvenile mortality. The data set included 7,000 woody perennials of 24 species in a mapped hectare of Joshua Tree National Monument, California. The site is dominated by *Ambrosia dumosa* (62.0% of the stems), with *Larrea tridentata* a conspicuous secondary species (2.3% of the stems). Analyses of static pattern for common species showed: (1) aggregated adults and juveniles for *Ambrosia dumosa*, *Eriogonum fasciculatum*, *Mirabilis bigelovii*, and *Sphaeralcea ambigua*, with more aggregation among juveniles than adults; (2) randomly distributed adults and juveniles for *Krameria grayi*, *Opuntia ramosissima*, *Simonsia chinensis*, and *Yucca schidigera*. The summed volumes and distances between nearest conspecific neighbors were positively correlated for *Ambrosia dumosa* and *Larrea tridentata*, but not significantly correlated for eight remaining species with ≥ 100 individuals. Static pattern suggests only weak evidence for negative interactions in *Ambrosia* and *Larrea*, and little evidence for other species. Alternative mechanisms other than negative interaction that could give rise to these static patterns are discussed. Juvenile mortality was documented for four common species (*Ambrosia dumosa*, *Eriogonum fasciculatum*, *Mirabilis bigelovii*, and *Sphaeralcea ambigua*) that experienced substantial mortality. Analyses show: (1) the proportion of individuals that died was independent of the initial density of conspecifics; (2) distance to conspecific adults did not differ for juveniles that died versus those that survived; and (3) death was no more likely for juveniles that contacted other plants than for those that were isolated. The exception was a vine, *Mirabilis bigelovii*, whose juveniles survived better in contact with other plants. In sum, neither spatial pattern nor patterns of mortality showed clear evidence of negative intraspecific interference.

Key words: Colorado Desert – Community ecology – Interference – Plant dispersion – Plant mortality

Interference may occur among the perennial plants of arid environments. Experiments demonstrate that desert perennials can reduce xylem water potentials and rates of growth and reproductive output of established neighbors (Fonteyn and Mahall 1981; Robberecht et al. 1983; Ehleringer 1984)

as well as rates of growth and survivorship of nearby seedlings (Friedman 1971; Sheps 1973). While these studies prove that interference can have negative consequences for interacting plants, the overall importance of interference is uncertain (Fowler 1986).

Most evidence for interference among desert plants comes from studies of the spatial distribution of individuals (hereafter dispersion). For the most part these studies infer interference from static dispersion. For example, a regular dispersion, in which plants are uniformly distributed like trees in an orchard, may indicate that interference has led to the death of neighbors that occurred too close together (Beals 1968; Woodell et al. 1969; Waisel 1971). These and other early observations and the subjective impression that desert shrubs are widely and regularly spaced led to the early consensus that interference was of wide significance among plants in arid environments. Anderson (1971) and Barbour (1973) questioned the consensus, noting that aggregated and random patterns of dispersion are much more frequent than regular patterns.

Two more involved patterns have also been seen as evidence of interference among plants in arid environments. First, a positive correlation between the summed sizes and distances between neighbors may indicate that interference among near neighbors has suppressed their growth (e.g., Yeaton and Cody 1976). Second, a change in the pattern of dispersion with size or age, with small plants being more aggregated in space and larger conspecifics being more regularly dispersed, may indicate that interference has led to the deaths of near neighbors as plants mature (e.g., Greig-Smith and Chadwick 1965; Phillips and MacMahon 1981). Alternative mechanisms that might generate these two patterns have apparently not been considered.

We examine the dispersions of 24 species of perennials over a mapped hectare of the northern Colorado Desert. We test for the two patterns described above, and we examine the spatial distribution of mortality of seedlings of four of the more common species over a one-year interval. Mechanisms other than interference that are consistent with the observed patterns are introduced. Some of the analyses have been applied to one species discussed here (*Sphaeralcea ambigua*; see Howe and Wright 1986). This paper provides a comparative analysis for a variety of shrub species of the northern Colorado Desert.

A secondary question is whether intraspecific interactions among dominant species are like those among subdominants. Because dominant species often grow near conspecifics, intraspecific interference might be far more important

for them than for less common species that usually grow near members of other species. A parallel analysis of heterospecific pattern and mortality will be forthcoming.

Methods

Description of site

The study site is on a bajada that slopes to the northwest of the Eagle Mountains in Joshua Tree National Monument (longitude 115°47'; latitude 33°46'). Elevation is 1006 m. Rainfall averaged 18.5 cm/yr at the nearby (2 km) Cottonwood Spring ranger station between 1970 and 1984; rainfall during 1984 was 16.5 cm. Approximately 62% of the individual shrubs are of one species (*Ambrosia dumosa*), while 2.3% are of the much larger creosote (*Larrea tridentata*). The site is within 10 km of the transition to Mojave Desert vegetation.

The site is almost free of topographic heterogeneity. The steepest slope parallels the bajada and is 4%. Runoff channels averaged 3.2 cm in depth, and the deepest channel was 13 cm. At nine sites at a depth of 10 cm, the soil consisted of an average of 29.8% gravel (particle diameter > 2 mm), 62.4% sand (0.05 mm < diameter ≤ 2 mm) and 7.8% clays (diameter ≤ 0.05 mm).

The site is virtually free of human disturbance. In particular, cattle have not grazed the site since 1940 (Greene 1983). Prior to 1940, a "small number" of cattle grazed at Cottonwood Spring from 1916 to 1917 and again in the late 1930's. Cattle grazed in larger numbers in the northwestern portion of Joshua Tree National Monument as early as 1870, and Cottonwood Spring was a frequent stop during transit (Greene 1983). The spring is 2 km from our study site.

Mapping

We mapped plants to the nearest 0.25 m using a grid of 1 square hectare (100 × 100 m), surveyed to subplots of 25 m² (5 × 5 m) between 15 March and 8 April 1984. This grid permitted analysis of contiguous quadrats of different areas (e.g., 25 m², 625 m²). Each plant was marked with a uniquely numbered aluminum tag, and was recorded by species, height and major and minor axes, reproductive condition, and coordinates on the 100 × 100 m grid. All above-ground contacts between mapped plants were noted. Depletion (death of marked plants) after one year was evaluated between 23 March and 3 April 1985. We also noted grazing damage on *Ambrosia dumosa* in 1985. Grazed plants were distinctively clipped by jackrabbits (*Lepus californicus*) leaving cut stems and flattened rather than rounded canopies.

Twenty-four perennial plant species were encountered. Nomenclature follows Munz (1968). For 22 species, we mapped individuals ≥ 10 cm tall. The exceptions are *Eriogonum fasciculatum*, for which we mapped all individuals, and the extremely abundant *Ambrosia dumosa*, for which we mapped individuals ≥ 10 cm tall over the first 750 m² subsample and individuals ≥ 20 cm tall over the remainder of the hectare. Analyses for *A. dumosa* are for the first 750 m² unless otherwise noted. Individuals < 10 cm tall that were not mapped were present for the following seven species: *A. dumosa*, *Encelia farinosa*, *Hymenoclea salsola*, *Mirabilis bigelovii*, *Opuntia echinocarpa*, *O. ramosissima* and *Sphaeralcea ambigua*.

For six species, it was sometimes difficult to distinguish neighboring individuals. Either several individuals were so close together that they appeared as a single individual or multiple stems of one individual were so far apart that they appeared as different individuals. To minimize both problems, we examined the rooted stems of every mapped plant. Identity of individuals was not a problem for 18 species because individuals almost invariably had a single stem. It was not possible to make unambiguous determinations for *Tetracoccus hallii*. Vegetative spreading occurred by surface suckers that decayed rapidly, leaving groups of stems whose mode of establishment was unknown. *T. hallii* is not considered further.

Three methods were used to map individuals of the five remaining species. For *Larrea tridentata* and *Yucca schidigera*, an arbitrary criterion distinguished individuals. Stems separated from all conspecific stems by ≥ 1 m were treated as separate individuals, and stems separated by < 1 m were treated as single individuals. For *L. tridentata*, this might combine some individuals (Wright 1970) and split others (Vasek 1980). For *Eriogonum fasciculatum* and *Salazaria mexicana*, we identified separate individuals by excavating between all conspecific stems separated by < 1 m. Excavations were 10 cm deep and were on the midpoint of the shortest line between the centers of neighboring stems. We replaced excavated soil.

Mapping criteria for *Ambrosia dumosa* were checked further. Excavations just outside of Joshua Tree National Monument demonstrated the extent of cloning and merger for *A. dumosa*. We excavated 30 pairs of stems that would have been mapped as two adults, 30 pairs of stems that would have been mapped as one adult and one juvenile, and 30 large, complex plants that would otherwise have been mapped as single individuals. We excavated to a depth of 30 cm.

Plant size and reproductive status

Plants were divided into two stage classes on the basis of their volumes and reproductive histories. Following Phillips and MacMahon (1981), we calculated volumes (V) as if plants were oblate spheroids so that

$$V = \pi a^2 b / 6,$$

where a is the smaller and b the larger of the height and the average of the major and minor axes.

The presence or absence of current or past reproductive structures (buds, inflorescences, infructescences) indicated sizes at which shrubs reproduced. We examined the relationship between the proportion of individuals that had such structures and plant volume. Sharp inflection points establish threshold volumes that separate non-reproductive juveniles from reproductive stages.

Static spatial pattern

Analysis 1: Nearest neighbor distances for all conspecifics. Donnelly (1978) provides expected values and variances of total nearest neighbor distances under the null hypothesis that individuals are randomly dispersed. Following Donnelly (1978), a standard normal deviate was calculated to test the null hypothesis. Three species were too rare for analysis.

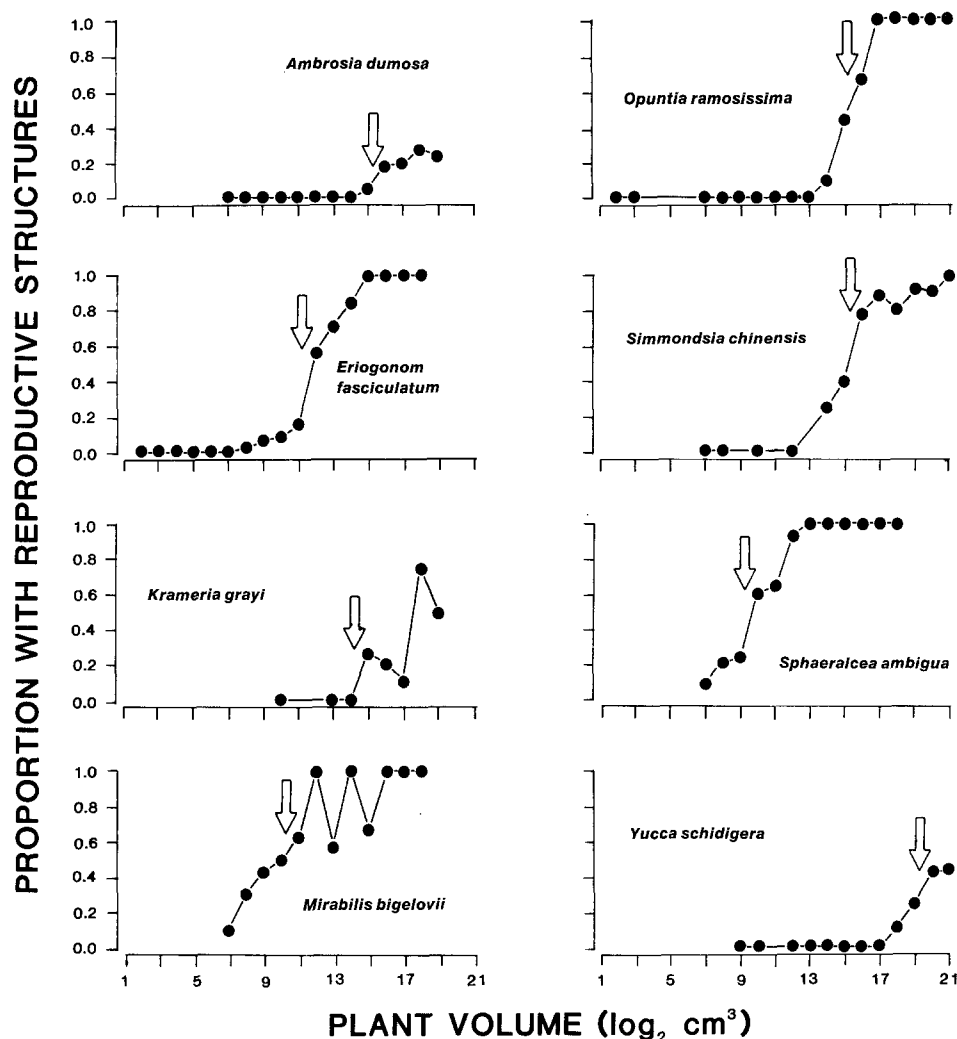


Fig. 1. Reproductive status as a function of plant volume. Reproductive status is plotted on the ordinate as the proportion of individuals in each volume category bearing reproductive structures. Arrows indicate volumes used to separate juveniles and adults. Sample sizes as in Table 1

Analysis 2. Quadrat counts. Morisita's index of dispersion was calculated from counts of individuals among quadrats of area, 2^xm^2 , where x takes all integer values between 2 and 7 for *Ambrosia dumosa* and 2 and 11 for all other species. The null hypothesis of random dispersion was evaluated with quadrats of 64m^2 (Morisita 1959). Separate calculations of Morisita's index for juveniles and adults determined whether the dispersion of juveniles and adults differed.

Analysis 3: Densities of juveniles and adults. The null hypothesis that densities of juveniles and adults were independent was tested for the eight species for which juveniles and adults could be distinguished (Fig. 1). The mapped hectare was divided into sixteen 625m^2 subplots ($25 \times 25 \text{m}$) and the number of juveniles in each subplot was regressed against the number of adults. For *Ambrosia dumosa*, the entire hectare was included and individuals $< 20 \text{cm}$ tall were excluded.

Analysis 4: Distribution of juveniles with respect to adults. The relative dispersion of juveniles and adults was evaluated with a test proposed by Hamill and Wright (1986). Briefly, the test compares observed and expected distances between juveniles and nearest conspecific adults. Let D_k represent the distance between juvenile k and the nearest conspecific

adult. For any distance d , define $F_O(d)$, the observed probability that $D_k \leq d$. Now,

$$F_O(d) = \sum_{k=1}^j I_k / J, \quad (1)$$

where J is the number of juveniles and I_k is an indicator variable which equals one if $D_k \leq d$ and zero otherwise.

Under the null hypothesis that juveniles are located independently and at random, the expected probability that a juvenile falls within a distance d of the nearest conspecific adult, $F_E(d)$, is simply the proportion of the mapped hectare that falls within distance d of the nearest conspecific adult. Let $D_{x,y}$ represent the distance between any point x, y and the nearest conspecific adult. Since we mapped plants to the nearest 0.25m , x and y take all values between zero and 100 that are multiples of 0.25 giving 401^2 possible locations. Now,

$$F_E(d) = \sum_{y=0,0.25}^{100} \sum_{x=0,0.25}^{100} I_{x,y} / 401^2,$$

where $I_{x,y} = 1$ if $D_{x,y} \leq d$ and zero otherwise. Note that $F_O(d)$ and $F_E(d)$ are probability density functions.

We calculated $F_O(d)$ and $F_E(d)$ from the 1984 map and used a two-tailed, one-sample Komolgorov-Smirnov test

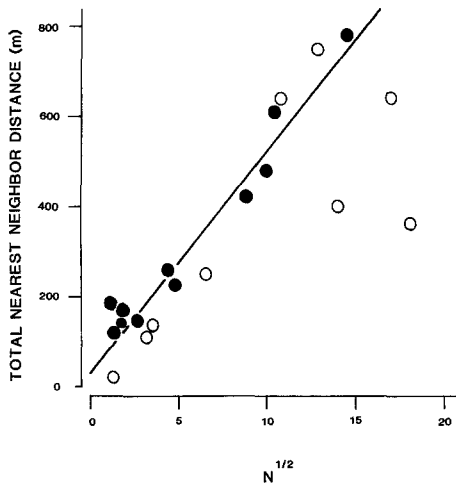


Fig. 2. Analyses of dispersion based on conspecific nearest neighbor distances (NND's). Total NND summed over all individuals is plotted against the square root of the number of individuals in the population (N). The solid line represents expected values of total NND were plants distributed at random (Donnelly 1978). Observed values that fall above and below the line represent populations that tend toward regular and aggregated distributions, respectively. Open circles represent populations that differ significantly from their expected total NND; closed circles represent populations that do not. *Ambrosia dumosa* is omitted because the area of analysis is smaller than for the other species giving a different relationship between N and total NND

to compare the distributions. Hamill and Wright (1986) discuss this test more fully and demonstrate its usefulness against a variety of non-random distributions.

Analysis 5: Distances between and sizes of nearest neighbors. Pielou (1960) first suggested that negative interference might cause a positive relation between the summed volumes and distances between neighboring plants. We tested the null hypothesis that the summed volumes and distances between nearest conspecifics were independent for the 10 species with ≥ 100 mapped individuals. To insure independent observations, no individual was included in more than one nearest neighbor pair. To correct for edge effects, all nearest neighbor pairs for which an individual fell within a distance x of the edge of the plot were omitted, where x is the longest observed nearest neighbor distance.

Analyses of mortality. Juvenile mortality (%) was recorded by itemizing dead marked plants after one year for the 4 species common enough for quantitative analysis: *Ambrosia dumosa* (15.1%), *Eriogonum fasciculatum* (8.9%), *Mirabilis bigelovii* (16.2%) and *Sphaeralcea ambigua* (25.4%). Virtually no adults died. We tested the hypotheses that: (1) deaths occurred independently of the local density of conspecifics, (2) deaths occurred independently of the position of the nearest conspecific adult, and (3) deaths (and for *Ambrosia dumosa* grazing damage) occurred independently of physical contact with neighboring plants of any species.

Weighted logistic regression (Neter and Wasserman 1974) was used to test the first null hypothesis with quadrats of three sizes (2.25, 4 and 16 m²). The independent variable was the number of conspecifics present in the quadrat in 1984. The dependent variable was the proportion of juve-

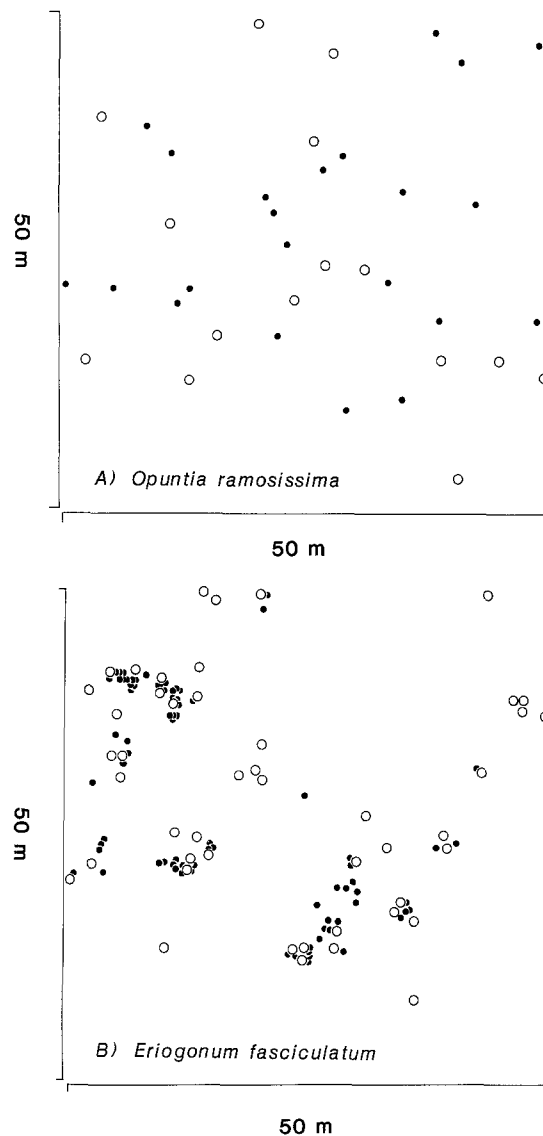


Fig. 3A, B. Representative maps of juveniles (closed circles) and adults (open circles) on one-fourth of the mapped hectare. **A** The overall dispersion of *Opuntia ramosissima* is uniform, and the dispersion of juveniles with respect to adults cannot be distinguished from random. **B** The overall dispersion of *Eriogonum fasciculatum* is aggregated, and juveniles are aggregated about adults

niles that died in each quadrat between 1984 and 1985. Quadrats lacking juveniles in 1984 were excluded.

To test the second null hypothesis, density functions were compared for distances between (1) juveniles that survived and the nearest conspecific adult and (2) juveniles that died and the nearest conspecific adult. Density functions were calculated from equation 1, and a two-tailed, two-sample Komolgorov-Smirnov test was used to compare them. Sample size equals the number of juvenile-adult distances in each density function. Contingency analyses were used to test the third null hypothesis.

Results

Excavations

For *Ambrosia dumosa*, four of the 30 "pairs" of stems that we would otherwise have mapped as two adults were joined

Table 1. Summary of analyses of dispersion for species in which adults and juveniles are easily distinguished^a

Species	Number of		Dispersion of all conspecifics ^b		Relative dispersion of juveniles and adults		
	Adults	Juveniles	Nearest neighbor distances	Quadrat counts	Quadrat counts ^c	Density correlated? ^d	Juvenile-adult distance ^e
<i>Ambrosia dumosa</i>	172	299	A ***	A **	J > A	P *	A **
<i>Eriogonum fasciculatum</i>	128	203	A ***	A **	J > A	P ***	A ***
<i>Mirabilis bigelovii</i>	129	69	A ***	A **	J > A	P **	A ***
<i>Sphaeralcea ambigua</i>	217	73	A ***	A **	J > A	NS	A ***
<i>Krameria grayii</i>	63	18	R	R	J ~ A	P **	R
<i>Opuntia ramosissima</i>	68	51	U *	R	J ~ A	NS	R
<i>Simmondsia chinensis</i>	191	28	R	R	J ~ A	NS	R
<i>Yucca schidigera</i>	71	42	R	R	J ~ A	NS	R

^a *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$

^b A aggregated, U regular, R random

^c J > A = Morisita's index greater for juveniles than for adults for all quadrat areas. J ~ A = Morisita's index indistinguishable for juveniles and adults

^d P positive, NS not significant

^e A juveniles aggregated about adults, R juveniles distributed randomly and independently. Analysis of Hamill and Wright (1986)

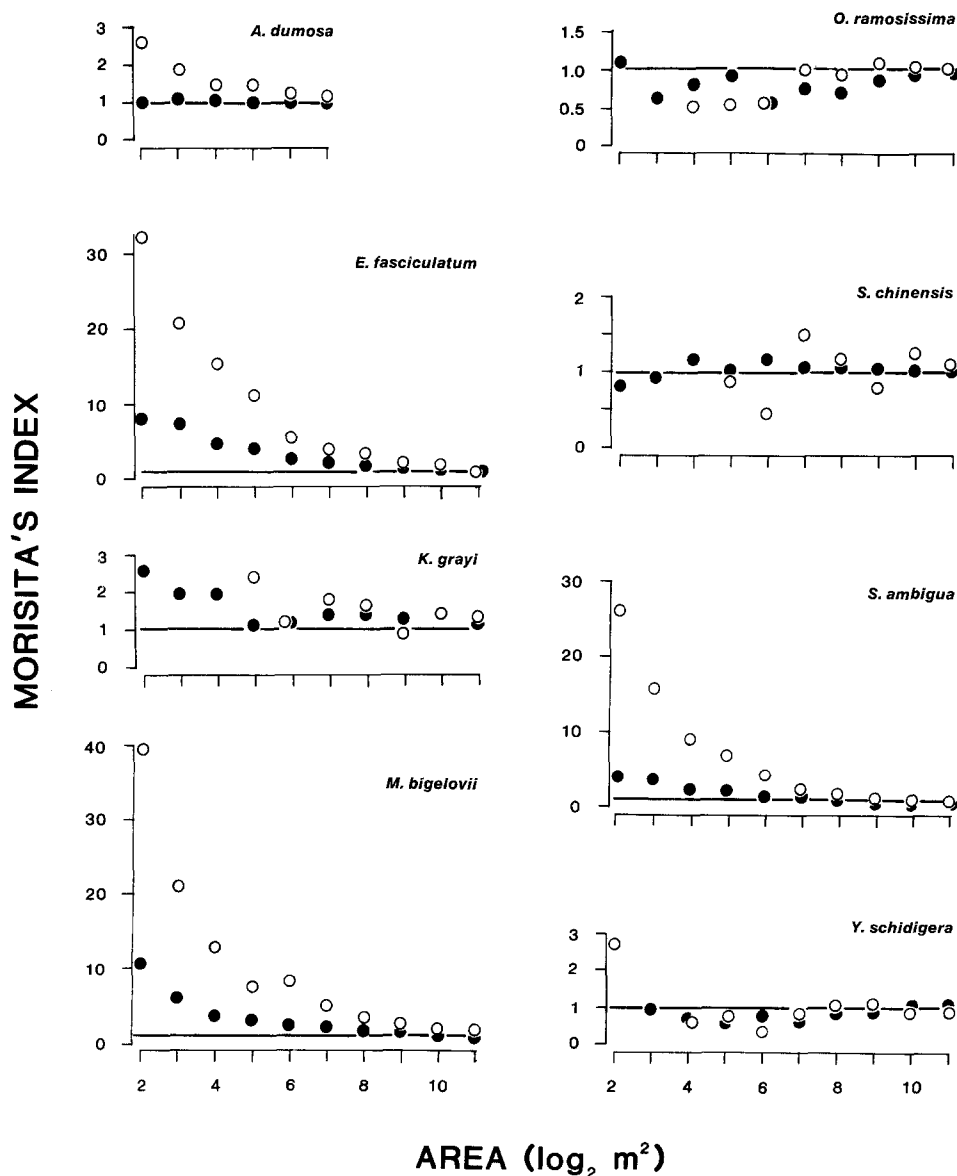


Fig. 4. Analyses of dispersion based on quadrat counts for species for which adults (closed circles) and juveniles (open circles) could be distinguished. Morisita's index is plotted on the ordinate. The logarithm of quadrat area is plotted on the abscissa. The index equals one (solid line in each plot) when plants are distributed at random, and takes values greater and less than one for aggregated and regularly dispersed populations, respectively

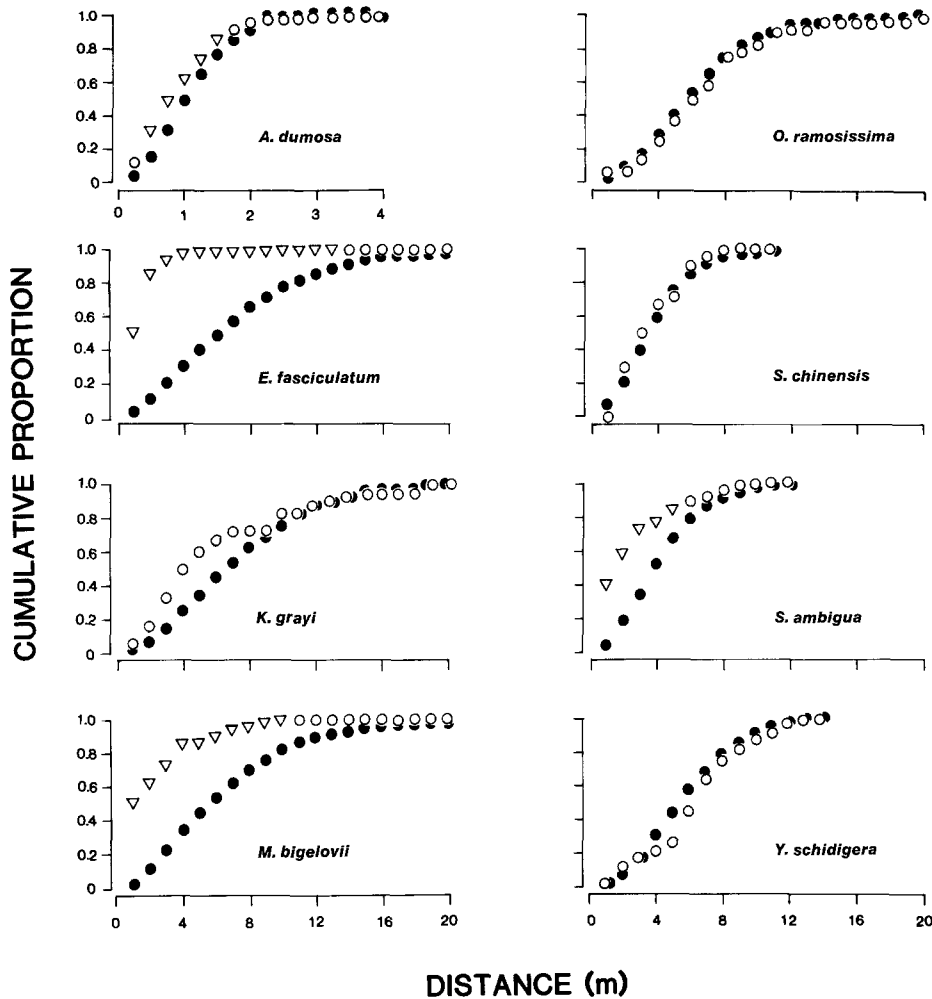


Fig. 5. Relative dispersion of adults and juveniles. Distance is plotted on the abscissa. The cumulative proportion of juveniles (open circles and triangles) and random points (closed circles) less than a given distance from the nearest conspecific adult is plotted on the ordinate. Observed distributions that include triangles are significantly different from their respective null distributions. When this occurs, juveniles are invariably found closer to conspecific adults than expected by chance. See text for further explication. The relatively small range of distances for *Ambrosia dumosa* reflects the smaller area analyzed and the high density of *A. dumosa*.

below the soil surface. Thus, splitting of adults is a potential problem. Excavation confirmed (30 for 30), however, that we identified single large individuals and neighboring adults and juveniles correctly.

To evaluate the effect of counting single individuals as more than one plant, we repeated our analyses for *Ambrosia dumosa* with all problematic stems included and centers of groups of problematic stems excluded, and vice versa. Results were robust with respect to the choice of analysis, and we only present results for the former.

Plant size and reproductive status

Reproductive status was related to plant size for 8 species (Fig. 1). Sample sizes were too small for the remaining species. For *Ambrosia dumosa*, *Krameria grayi*, and *Yucca schidigera*, fewer than 100% of the largest individuals bore reproductive structures. Macroscopic evidence of past reproduction may have been lost from large individuals of these species, and all individuals larger than the thresholds indicated in Fig. 1 are considered to be adults. The proportion of individuals that bore residual reproductive structure increased with plant size for these 8 species and included a sharp threshold for most. The presence of a sharp threshold indicates the attainment of reproductive stage, even when macroscopic evidence is lacking for some plants in the sample.

Dispersion

Analysis 1. Nearest neighbor distances for all conspecifics. The analyses of nearest neighbor distances indicate that dispersion spans the continuum from regular to highly aggregated (Figs. 2, 3). *Larrea tridentata* and *Opuntia ramosissima* were apparently regularly distributed. The regular dispersion of *L. tridentata* is suspect because stems separated by <1 m were arbitrarily considered to be single individuals. Individuals of the following species were aggregated in space: *A. dumosa* (-10.7), *Encelia farinosa* (-2.0), *Eriogonum fasciculatum* (-20.4), *Matelea parviflora* (-3.1), *Mirabilis bigelovii* (-11.5), *Porophyllum gracile* (-2.0), *Salazaria mexicanum* (-3.5), and *Sphaeralcea ambigua* (-8.3). The number in parentheses is the standard normal deviate proposed by Donnelly (1978).

Analysis 2. Quadrat counts. Analyses of quadrat counts based on Morisita's index with quadrats of 64 m² and analyses of nearest neighbor distances (Analysis 1) gave very similar results with adults and juveniles combined (Table 1). The only differences are that analyses of quadrat counts did not reject the null hypothesis of random dispersion for *Larrea tridentata*, *Opuntia ramosissima*, and species with fewer than 25 individuals.

Morisita's index declines steadily with increasing quadrat size whenever dispersion is aggregated (Fig. 4). This de-

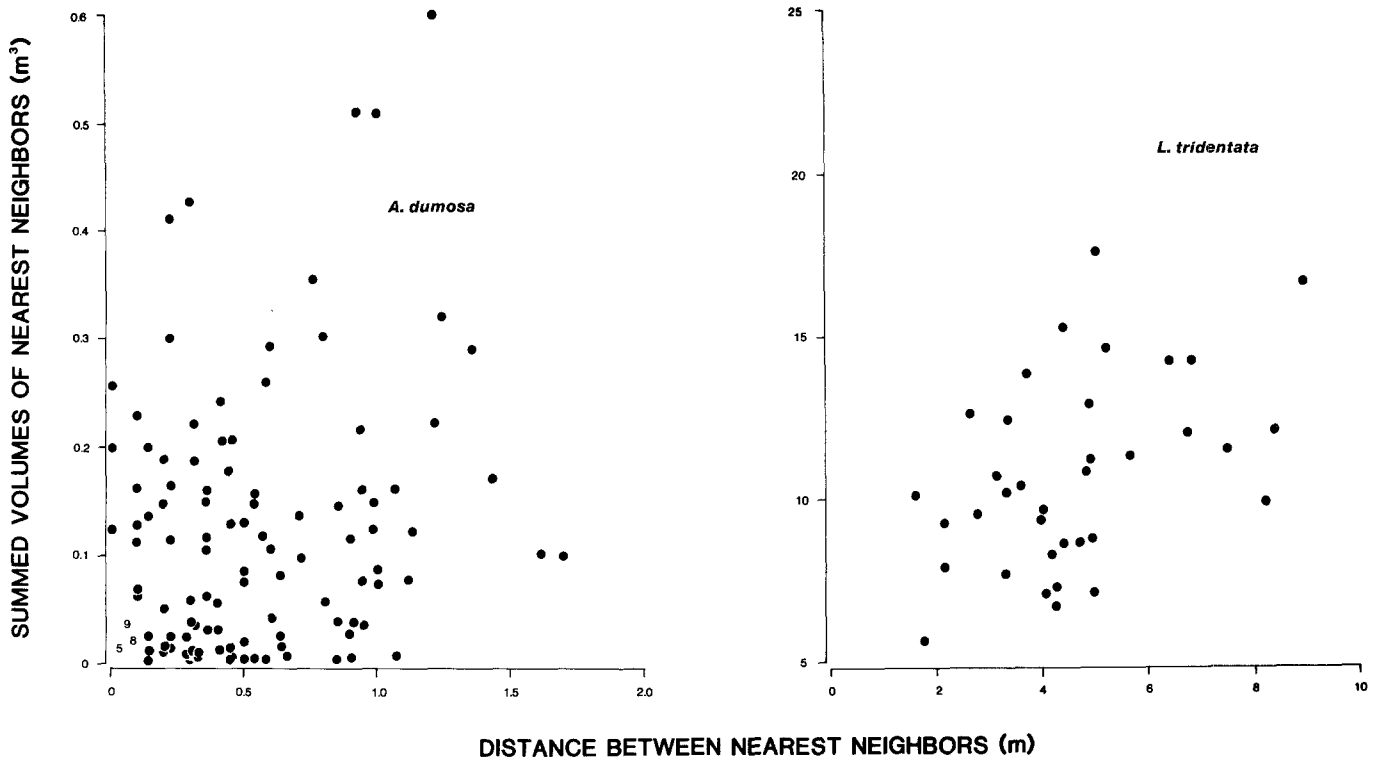


Fig. 6. Correlation between the summed volumes and distances between nearest conspecific neighbors for *Larrea tridentata* ($r=0.45$, $P<0.01$) and *Ambrosia dumosa* ($r=0.32$, $P<0.001$). Numbers refer to multiple neighbor pairs with similar summed volumes and distances

cline indicates that individuals occur in clumps and the dispersion of individuals within clumps is random (Morisita 1959).

When juveniles and adults are analyzed separately, three patterns emerge (Fig. 4). First, for *Eriogonum fasciculatum*, *Mirabilis bigelovii* and *Sphaeralcea ambigua*, juveniles and adults are both aggregated, and juveniles are more aggregated than adults. Second, for *Krameria grayi*, *Opuntia ramosissima*, *Simmondsia chinensis* and *Yucca schidigera*, juveniles and adults are both randomly distributed, and there are no consistent differences between juvenile and adult dispersion. Third, for the 750 m² for which we mapped all individuals ≥ 10 cm tall, juveniles of *Ambrosia dumosa* are aggregated while adults are randomly distributed. If the entire hectare is included, however, the dispersion of adults of *A. dumosa* is aggregated.

Analysis 3: Densities of juveniles and adults. Numbers of juveniles and adults in 625 m² subplots were positively correlated for *Ambrosia dumosa* ($P<0.01$), *Eriogonum fasciculatum* ($P<0.0005$), *Krameria grayi* ($P<0.01$) and *Mirabilis bigelovii* ($P<0.005$). The correlation was not significant for *Opuntia ramosissima*, *Simmondsia chinensis*, *Sphaeralcea ambigua* and *Yucca schidigera*.

Analysis 4: Distribution of juveniles with respect to adults. The null hypothesis that juveniles are distributed independently and randomly was rejected for *Ambrosia dumosa* ($P<0.01$), *Eriogonum fasciculatum* ($P<0.001$), *Mirabilis bigelovii* ($P<0.001$), and *Sphaeralcea ambigua* ($P<0.001$). For these species, juvenile-adult distances are consistently shorter than expected (Fig. 5). The null hypothesis was not rejected for *Krameria grayi*, *Opuntia ramosissima*, *Simmondsia chinensis* and *Yucca schidigera*.

Analysis 5: Distances between and sizes of nearest neighbors. The summed volumes and distances between nearest neighbors were positively correlated for *Ambrosia dumosa* ($r=0.32$, $P<0.001$) and *Larrea tridentata* ($r=0.45$, $P<0.01$, Fig. 6). The correlation was not significant for the 8 remaining species with ≥ 100 individuals (all $P>0.14$).

Mortality

Mortality of juveniles of *Ambrosia dumosa*, *Eriogonum fasciculatum*, *Mirabilis bigelovii* and *Sphaeralcea ambigua* provides no evidence for negative interference. The proportion of individuals that died was independent of the initial density of conspecifics ($P>0.10$) at all spatial scales tested for all four species. Distance to the nearest conspecific adult did not differ for juveniles that survived and juveniles that died ($P>0.10$, Fig. 7). The frequency of death was similar for juveniles that were initially isolated from all other plants and for juveniles that contacted another plant for *A. dumosa*, *E. fasciculatum* and *S. ambigua* ($P>0.10$, Table 2). This was also true for grazing damage and for contacts with conspecifics and heterospecifics for *A. dumosa* (Table 2).

For *Mirabilis bigelovii*, a vine that uses shrubs for support, the frequency of death was greater for juveniles that were initially isolated than for juveniles that initially contacted another plant ($P=0.022$, Fisher Exact Test, Table 2). Adults of *M. bigelovii* are also positively associated with other species (Wright and Howe, unpublished work).

Discussion

Static dispersion generates three kinds of evidence that have been used to infer negative interaction among conspecific

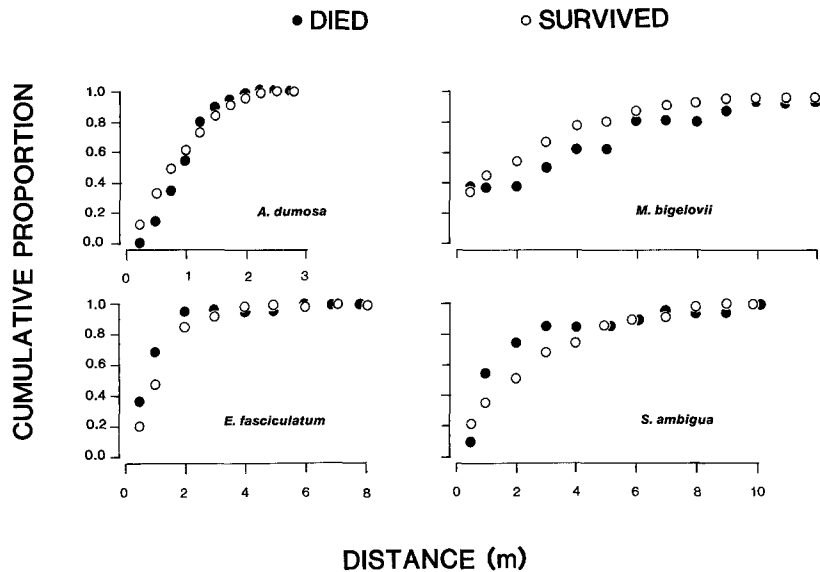


Fig. 7. Mortality and survivorship of juveniles related to distance to the nearest conspecific adult. Distance is plotted on the abscissa. The cumulative proportion of juveniles that died (closed circles) and that survived (open circles) less than a given distance from the nearest conspecific adult is plotted on the ordinate. There are no significant effects of isolation on survivorship

Table 2. Mortality of juveniles related to physical contact with other conspecifics and heterospecifics

	<i>Ambrosia dumosa</i> ^a			<i>Eriogonum fasciculatum</i>		<i>Mirabilis bigelovii</i>		<i>Sphaeralcea ambigua</i>	
	Alive	Dead	Grazed	Alive	Dead	Alive	Dead	Alive	Dead
Solitary Contact	56	7	7	117	12	4	4	20	10
Conspecific	56	12	6	38	3	0	0	1	0
Heterospecific	37	11	7	30	3	79	12	32	8

^a Only juveniles ≤ 20 cm tall are included. No deaths occurred among larger juveniles

plants. These are: (1) regular dispersion, (2) positive correlations between the intensity of dispersion and plant size, and (3) positive correlations between the summed sizes and distances to nearest neighbors. Because mechanisms other than interference might produce each of these results, static pattern is best integrated with (4) analyses of mortality that show whether the risk of death depends on proximity to conspecifics.

Regular dispersions

Spatial regularity is unusual in our sample as well as in the literature (Anderson 1971; Barbour 1973). This may be true because negative interactions can only cause regular dispersions under unusual circumstances. First, seeds and sites favorable for growth and germination must be so common that seedling establishment is widespread. Then deaths caused by negative interactions must ensue, and survivors must be regularly distributed. Fonteyn and Mahall (1981) add that regular patterns are still unlikely unless recruitment of seedlings is a rare event because seedlings usually occur in clumps. For these reasons, regular patterns represent an extreme and unlikely outcome of interaction (Anderson 1971; Barbour 1973). The absence of spatial regularity has little to say about the presence or absence of interference.

Alternative mechanisms can also generate regular patterns. For example, seeds might be dispersed to regularly dispersed sites such as ant colonies or germination and seed-

ling growth might require conditions that are present in regularly dispersed sites. This might occur, for instance, if seedlings require the protection of the large clumps of plants that are approximately regularly distributed over our mapped hectare. Consequently, even the occurrence of regular spacing need not, by itself, suggest competition.

Intensity of dispersion and plant size

A more frequent observation is that small plants are aggregated in space while larger conspecifics are randomly or even regularly dispersed. Correlations between plant size and dispersion occur in arid environments and have generated the following inference: as small plants in dense clumps grow they interfere with one another causing density-dependent mortality which leaves survivors that are larger and more widely spaced (e.g., Greig-Smith and Chadwick 1965; Anderson et al. 1969; Phillips and MacMahon 1981). This inference has become so routine that it has been applied in reverse. Gulmon et al. (1979) found no correlation between plant size and dispersion and, from this and other evidence, inferred that negative interactions were unimportant in their study population.

We observed the familiar correlation for four species. Juveniles were more intensely aggregated than adults for *Ambrosia dumosa*, *Eriogonum fasciculatum*, *Mirabilis bigelovii* and *Sphaeralcea ambigua* (Fig. 4). Yet, for these same four species, mortality of juveniles occurred independently of density of conspecifics, and of distance to the nearest

conspecific adult (Fig. 7). For all but *M. bigelovii*, mortality of juveniles was independent of physical contact with neighbors (Table 2). We cannot discount the possibility that density-dependent mortality might occur at some later date as juveniles mature, but observed mortality belies the inference that density-dependence accompanies correlations between plant size and dispersion.

More general objections to inferences based on correlations between plant size and dispersion also exist. First, the inference requires an implicit assumption that the population is in steady state. If the population is not in steady state, its dispersion may change with time. The present dispersion of juveniles could lead to some future dispersion of adults that is different from the present dispersion. This assumption obviously cannot be evaluated in a short-term study.

An equally important objection is that alternative biological mechanisms have not been considered. For instance, seed-eaters, herbivores, and pathogens may kill a disproportionate number of seeds and seedlings in dense patches (e.g., Howe and Smallwood 1982; Augspurger and Kelly 1984). After such density-dependent mortality, survivors will be less intensely aggregated. With growth of survivors and subsequent seedling recruitment, the familiar correlation between plant size and dispersion could emerge without plant-plant interference.

Moreover, mortality may be caused by established neighbors rather than by interference among small juveniles. Small plants are frequently aggregated around conspecific adults (Fig. 5). Interference with a larger plant may cause mortality among its smaller neighbors (Friedman 1971; Sheps 1973; Friedman and Orshan 1975) thereby reducing the intensity of dispersion of survivors. Negative interference is responsible, but the outcome is asymmetrical, favoring established individuals.

Finally, sampling biases can affect the relationship between plant size and dispersion. Seedling recruitment occurs in different places in different years. Small plants will be restricted to the few sites where recent establishment has been successful. Larger plants may occur in more sites and be less aggregated simply because more year classes and more germination sites are sampled. These are plausible conditions in nature, especially for long-lived species. Numbers of cohorts will tend to be greater for large plants than for small plants for long-lived species because members of many cohorts will persist as larger individuals.

In sum, the inference that negative interactions underlie correlations between the intensity of dispersion and plant size is suspect. The correlation is consistent with several mechanisms and there is no reason to emphasize interference among maturing plants.

Summed sizes and distances between nearest neighbors

Negative interaction might cause a direct relation between the summed sizes and distances between pairs of interacting neighbors, with progressively larger plants suppressing neighbors over progressively larger areas (Pielou 1960). The fact that the summed sizes and distances between nearest neighbors are positively correlated for 24 of the 35 desert populations previously examined (Yeaton and Cody 1976; Yeaton et al. 1977; Fonteyn and Mahall 1981; Phillips and MacMahon 1981; Wright 1982) suggests that intraspecific interference may be of wide significance among desert

plants. In our study, however, the positive relationship between size and distance only holds for the two co-dominant species, *Larrea tridentata* and *Ambrosia dumosa* (Fig. 6).

In fact, there is a significant association between the dominance status of a species and the occurrence of positive correlations between the summed sizes and distances between nearest conspecific neighbors. Significant correlations exist for 20 of 30 dominant populations but for only 3 of 12 subdominant populations (Yeaton et al. 1977; Fonteyn and Mahall 1981; Phillips and MacMahon 1981; Wright 1982; this study). The difference in frequency of correlation between dominants and subdominants is significant ($X^2 = 4.44$, $P < 0.05$). Negative interference is probably more important among dominants because interference occurs among near neighbors. Near neighbors of dominant species are likely to include conspecifics while near neighbors of rarer species are likely to include heterospecifics.

There is at least one mechanism in addition to negative interaction that could cause positive correlations between the summed sizes and distances between nearest neighbors. When seedlings occur in dense aggregations, there will be many pairs of nearest neighbors that are both small and separated by very short distances. These pairs will fall close to the origin of a scatter plot of the summed sizes and distances between nearest neighbors (e.g., Fig. 6). If interference does not occur, older plants will occur as widely scattered observations on the same plot. A cluster of observations that fall close to the origin (seedlings) might introduce a positive correlation when superimposed on widely scattered observations in the positive portion of coordinate space (older plants). A positive correlation between the summed sizes and distances between nearest neighbors could in this way occur as an artifact of initial seedling distribution in the absence of negative interference.

Ambrosia dumosa provides an example of a species in which a positive correlation between summed sizes and nearest neighbor distance may not be due to negative interference. The dispersion of small individuals is aggregated (Fig. 4). When individuals are divided into three size categories that include equal numbers of plants, the number of nearest neighbor pairs that includes two small individuals is significantly greater than expected by chance ($X^2 = 4.34$, $P < 0.05$). Finally, the scatter plot of summed sizes and distances between nearest neighbors includes a cluster of observations close to the origin and little additional indication of correlation (Fig. 6). We conclude that negative interference might occur among individuals of *A. dumosa*, but the observed correlation (Fig. 6) is also consistent with a noninteracting population in which juveniles are aggregated for unknown reasons.

To summarize, the two types of evidence most frequently used to infer negative interference from the dispersion of plants in arid environments are both consistent with mechanisms that do not involve negative interference. Interference may occur, as shown by experiments cited earlier. What is not clear is whether negative interference among members of the same species is of widespread importance in stands of mixed age.

Mortality and dispersion

For the four species for which appreciable mortality was observed, deaths occurred independently of the local density of conspecifics and of distance to the nearest conspe-

cific adult (Fig. 7). If mortality is density independent, as these data suggest, the dispersion of adults should mirror the dispersion of juveniles. This is the case for the eight species for which juveniles and adults could be distinguished (Table 1). When adults are aggregated in space, juveniles are also aggregated ($P=0.014$, Fisher Exact Test). Moreover, when adults are aggregated, local densities of juveniles and adults are positively correlated (*Sphaeralcea ambigua* is an exception; see Howe and Wright 1986), and juvenile-adult distances are shorter than expected by chance. A map of a representative quarter of the study hectare illustrates this pattern for *Eriogonum fasciculatum* (Fig. 3b). On the other hand, when adults are randomly or regularly distributed, juvenile and adult dispersion cannot be distinguished, local densities of juveniles and adults are independent (*Krameria grayi* is an exception), and juvenile-adult distances cannot be distinguished from chance. A map of a representative quarter of the study hectare illustrates this pattern for *Opuntia ramosissima* (Fig. 3a).

The following scenario might explain how juvenile establishment determines adult dispersion. Juveniles either become established in dense clusters close to conspecifics or independently of conspecifics (Figs. 3, 5). Subsequent mortality occurs independently of proximity to conspecifics and preserves the pattern set by early establishment.

Alternatively, the association between juvenile and adult dispersions may be an artifact of sample sizes. If adults and juveniles are treated as separate populations, dispersion tends to be aggregated for larger populations and random for smaller populations ($P=0.002$, Mann-Whitney U, abundances from Table 1, dispersions from Fig. 4). And the smaller populations tend to be juveniles and adults of the four species for which juveniles and adults are both randomly dispersed (Table 1).

In short, static pattern by itself does not provide much insight into the importance of interference in our study populations. Combined with monitoring of growth and survivorship, however, pattern analysis might distinguish among alternative interpretations of interactions among desert plants. Future recensuses may yet indicate that interference is important.

Acknowledgements. We thank R. Moon, W. Speckler and the staff of The Joshua Tree National Monument for their cooperation. The National Geographic Society, the University of Iowa, and the Research Opportunities Fund of the Smithsonian Institution provided financial support.

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