

Spatial patterns of mortality in a Colorado desert plant community

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Abstract

Spatial pattern and patterns of mortality were analyzed from a five year re-census of over 7 000 mapped perennial shrubs within a one hectare study plot in Joshua Tree National Park. A five year interval revealed evidence for negative intraspecific interactions which was not evident after a one year evaluation of the same plants within the study area. Juvenile mortality was a positive function of conspecific density for *Ambrosia dumosa*, *Eriogonum fasciculatum* and *Sphaeralcea ambigua*. In addition, juvenile *E. fasciculatum* that died occurred closer to conspecific adults than would be expected by chance. The two censuses are similar in that uniform patterns of distribution among conspecifics are rare, particularly for non-succulent species.

These results emphasize the value of mapped study sites in allowing dynamic inferences from otherwise static analyses. Herbivory and nurse effects are implicated as potential factors influencing the dispersion of perennial plants within deserts.

Introduction

Study of spatial pattern has contributed to the understanding of desert communities, first in indicating the likelihood of competition among plants (Beals 1968; Barbour 1969, 1973; Woodell et al. 1969; Anderson 1971), and secondly in suggesting competition, even in aggregated distributions where juveniles are more clumped than adults (see Greig-Smith & Chadwick 1965; Wright & Howe 1987). Competition is likely to be a dominant interaction among plants due to limiting water in deserts and the apparent uniform distribution of desert plants. Experiments have supported intra- and interspecific competition in some situations (e.g., Phillips & MacMahon 1981; Ehleringer 1984; Manning & Barbour 1988), and have suggested positive interactions among individuals, such as nurse effects in which juvenile survivorship is increased due to close association with adult plants of certain species in others (e.g., Turner et al. 1966; Steenbergh & Lowe 1969).

Both static pattern analyses and these experimental studies use single evaluations of pattern to help understand plant interactions which are dynamic pro-

cesses. As illustrated by insightful long-term studies of mapped trees in tropical rainforests (Hubbell 1979; Condit et al. 1992; O'Brien et al. 1995), monitoring mapped individuals over time allows for long term studies of changes in plant distributions and gives greater insight into the processes influencing plant dispersion. Most importantly, multiple censuses of mapped plants generate data on spatial variation of the demographic processes of mortality and recruitment (e.g., Clark & Clark 1984).

In an attempt to more closely follow the spatial dynamics of desert plants and to evaluate the role of intraspecific interference, over 7 000 individually tagged perennials within one hectare in southern Joshua Tree National Park, California were mapped in 1984, and the mortality of these plants was evaluated one year later (Howe & Wright, 1986; Wright & Howe, 1987). Analyses of intraspecific spatial patterns from the 1984 census indicated that of the most abundant species, four were clumped as adults and juveniles, with more aggregation among juveniles than adults (*Ambrosia dumosa*, *Sphaeralcea ambigua*, *Eriogonum fasciculatum*, *Mirabilis bigelovii*), four

species were randomly distributed (*Krameria grayi*, juvenile *Opuntia ramosissima*, *Simmondsia chinensis*, *Yucca schidigera*), and two species were uniformly distributed (adult *Larrea tridentata*, *Opuntia ramosissima*). After one year, spatial pattern did not reflect patterns of juvenile mortality, and consequently did not yield evidence for intraspecific interference for the majority of the species represented.

Here we re-evaluate intraspecific spatial patterns of dispersion and juvenile mortality of common species at this site five years after the original 1984 census. Because plant dispersion and plant density may vary with spatial scale, we use several tests to evaluate conspecific dispersion within the hectare as a whole, and within sub-quadrats of increasing area with juveniles and adults analyzed separately. We expect that a five-year interval should demonstrate changes in species dispersion over time and changes in patterns of mortality within the initial 1984 population which will either be consistent with the one-year findings that downplay the role of intraspecific competition, or will suggest other processes. We will test for: (1) overall patterns of dispersion that suggest competitive interactions over time; and (2) patterns of recruitment and mortality consistent with competitive interactions. Disproportionately high mortality of juveniles near adults, or uniform distribution of individuals within species, suggests strong competition among conspecifics. Absence of these patterns implies other processes which will be discussed where appropriate.

Study site and methods

Description of study site and species

The study site, within Joshua Tree National Park near Cottonwood Springs (longitude 115°47'; latitude 33°46'), is located on a featureless bajada (1–4% slope) of the Eagle Mountains, just south of the Colorado Desert interface with the Mojave Desert. The site is located approximately 3 km from public campgrounds, and is within a protected wilderness area with no trail access. Annual precipitation averages 18.5 cm. The soils, averaged from nine sites at a depth of 10 cm, consist largely of sand (62.4%), gravel (29.8%) and clays (7.8%). Grazing has not occurred at the site since 1940 (Greene 1983). Before 1940, there was light grazing from 1916 to 1917, and again in the late 1930s.

Twenty-four perennial plant species were encountered. Nomenclature follows Munz (1974). The majority

of the species are shrubs, with the exception of two species of cactus (*Opuntia echinocarpa* and *O. ramosissima*), and the succulent tree *Yucca schidigera*. Approximately 62% of individuals are of *Ambrosia dumosa* while the creosote bush (*Larrea tridentata*) represents 2.3%. Of these species, eight (*A. dumosa*, *Eriogonum fasciculatum*, *Krameria grayi*, *Mirabilis bigelovii*, *Opuntia ramosissima*, *Simmondsia chinensis*, *Sphaeralcea ambigua*, and *Yucca schidigera*) presented sufficient numbers of both juveniles and adults to allow for quantitative analysis. All of these species are associated with creosote bush scrub. Because it is a vine like species very rarely encountered without the physical support of another species, *M. bigelovii* was not included in the present study. A brief description of the focal species of this study follows.

Ambrosia dumosa [Asteraceae] is a drought deciduous shrub of moderate height (20–60 cm) which is abundant on well drained soils below 1061 m elevation. Lifespan has been reported to be from 35 to > 200 years (Bowers et al. 1995). *Eriogonum fasciculatum* [Polygonaceae] is a low lying shrub of moderate height (60–120 cm) commonly found on dry slopes. *Sphaeralcea ambigua* [Malvaceae] averages 20–60 cm and is associated with dry rocky slopes, mostly below 1212 m. *Simmondsia chinensis* [Buxaceae] is a 1–2 m dioecious shrub with persistent leaves common on dry slopes below 1515 m. *Opuntia ramosissima* [Cactaceae], a free branching cactus ranging in height from 30–150 cm, is common in dry washes below 1212 m. Arborescent *Yucca schidigera* [Agavaceae] occurs commonly on dry rocky slopes below 1515 m and is from 1–4.5 m tall. *Krameria grayi* [Krameriaceae] ranges from 30–70 cm in height and is associated with dry sandy and rocky places < 1212 m.

Plants were mapped between 15 March and 8 April 1984. Each individual was mapped to the nearest 0.25 m within a square hectare (100 × 100 m) which was divided into 5 × 5 m subplots. Each plant was marked with an aluminum tag, and was identified by its species, height, major and minor axes, reproductive status and its location on the 100 × 100 m grid. During the original census, plants ≥ 10 cm tall were mapped with two exceptions. For *Eriogonum fasciculatum*, all individuals were mapped, and for *Ambrosia dumosa*, which is extremely abundant, individuals ≥ 10 cm tall were mapped only in the first 750 m², and individuals ≥ 20 cm tall were mapped over the remainder of the hectare. Recruitment (referring to the appearance

of new juveniles), growth and mortality for the major species were recorded.

Determination of reproductive status

Plants were designated as juvenile or reproductive based on volumes and reproductive histories. Following Phillips and MacMahon (1981), we calculated volume (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 versus the average of the major and minor axes.

The presence or absence of past or present buds, inflorescences or infructescences were noted in addition to the size of the plant. We then plotted the proportion of individuals within a species with reproductive structures as a function of plant volume. Sharp inflection points established the threshold volumes used to separate juveniles from adults (Wright & Howe 1987).

Description of analyses

Parallel analyses of conspecific spatial patterns and mortality for the major species analyzed in 1985 were conducted using the results of the 1989 census. Mortality analyses consider only those juveniles which were present in 1984, and do not include new recruits. All other analyses include all juveniles. As noted in the earlier publication, conspecific analyses for *A. dumosa* are for the first 750 m², unless otherwise noted. Analyses were as follows:

(1) Mortality was analyzed for the three species common enough in the 1984 cohort for quantitative analysis (*Eriogonum fasciculatum*, *Sphaeralcea ambigua*, *Ambrosia dumosa*). Two tests evaluated the extent to which juvenile mortality was a function of local density of conspecifics or distance to the nearest conspecific adult. New juveniles were not included in these analyses. The first analysis (a) tested whether deaths of juveniles occurred independently of the local density of conspecifics at scales of 2.25, 4, and 16 m² in accordance with the previous study (Wright & Howe, 1987). Delimited areas which did not include juveniles in 1984 were not included in the analysis. Weighted logistic regression used the number of conspecifics present in 1984 as the independent variable, and the proportion of juveniles that died within each quadrat between 1984 and 1989 as the dependent variable. A second mortality analysis (b) tested whether juvenile deaths occurred independently of the distance

to the nearest conspecific adult, using a two-sample, two-tailed Kolmogorov-Smirnov test to compare the cumulative proportions of dead and surviving juveniles at increasing distances from adults (Hamill & Wright 1986; see below).

(2) Nearest neighbor distances were calculated to evaluate plant dispersion of all conspecifics within the study area using Donnelly's (1978) method. This test uses the total number of conspecifics within a given area to calculate the expected values and variances of total nearest neighbor distances, using the null hypothesis that individuals are randomly dispersed.

(3) The distribution of juveniles with respect to conspecific adults was tested using the methods of Hamill & Wright (1986). This test contrasts the cumulative distribution of juveniles within particular distance intervals to adults with a null distribution obtained from the distance of all points at every 0.25 m (401² possible points, including the origin) to adults within the study area. The equation for the null curve for *A. dumosa*, for which conspecific analyses are confined to the first 750 m², has a denominator of 12 221 (101 × 121 possible points). This method assesses the extent to which juvenile distribution is independent of adult distribution. In this analysis, D_k is the distance between juvenile k and the nearest conspecific adult. The observed proportion of juveniles within distance D_k at distance d is defined as

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

where J equals the number of juveniles and $I_k = 1$ if $D_k \leq d$, and zero otherwise. The expected curve is defined as

$$F_E(d) = \sum_{y=0.025}^{100} \sum_{x=0.025}^{100} I_{x,y} / 401^2,$$

where $I_{x,y} = 1$ if $D_{x,y} \leq d$ and zero otherwise. $D_{x,y}$ represents the distance between any point x, y and the nearest conspecific adult. Differences between juvenile and adult (null) curves were tested using a one sample, two-tailed Kolmogorov-Smirnov test. If juveniles are distributed randomly in relation to adults, there should be no significant difference between the juvenile and null distributions.

(4) Densities of juveniles and adults were calculated for quadrats of 625 m². Regression tested whether the number of juveniles was independent of the number of adults within these subplots.

Table 1. Demographic data

(a) Number of adult and juvenile plants present in 1984 and 1989. Dead plants are marked individuals which died between the 1984 and 1989 censuses

Species	1984		1989		Dead
	Adults	Juveniles	Adults	Juveniles	
<i>Ambrosia dumosa</i> *	172	299	186	553	60
<i>Eriogonum fasciculatum</i>	128	203	203	227	29
<i>Krameria grayi</i>	63	18	72	41	1
<i>Opuntia ramosissima</i>	43	76	83	139	1
<i>Sphaeralcea ambigua</i>	217	73	99	188	139
<i>Simmondsia chinensis</i>	191	22	203	42	0
<i>Yucca schidigera</i>	71	42	74	76	0

(b) Recruitment and mortality from 1984 through 1989. Percent juvenile mortality was calculated considering the number of juveniles originally present in 1984

Species	1989 mortality		% Juvenile mortality	Recruits
	Juvenile	Adult		
<i>Ambrosia dumosa</i>	59	1	19.73	298
<i>Eriogonum fasciculatum</i>	25	4	16.89	148
<i>Krameria grayi</i>	1	0	**	32
<i>Opuntia ramosissima</i>	1	0	**	101
<i>Sphaeralcea ambigua</i>	28	111	37.83	164
<i>Simmondsia chinensis</i>	0	0	**	23
<i>Yucca schidigera</i>	0	0	**	35

*Subsample of 750 m²

**percentages insignificant.

(5) Morisita's index of dispersion (Morisita 1959) was calculated using the number of conspecifics within quadrats of 2^x m², where x ranges from 2 through 7 for *A. dumosa* and from 2 through 11 for all other species. Juvenile and adult distributions were measured separately to evaluate whether or not their distributions differed. Morisita's index allowed us to measure the degree of clumping within a species and also to obtain an evaluation of the distribution of clumps within the entire study area.

Results

During the interval from 1984 to 1989, both adults and juveniles of most species increased in number, with far more mortality among juveniles than adults (Table 1).

(1) *Mortality: Analysis a.* Weighted logistic regression reveals that mortality of juveniles that were present in 1984 is positively associated with the local density of juvenile and adult conspecifics for *E. fasciculatum* at all spatial scales (2.25 m², $p < 0.005$; 4 m²,

$p < 0.001$; 16 m², $p < 0.005$), for *A. dumosa* in 2.25 m² ($p < 0.001$) and 4 m² ($p < 0.001$) quadrats, and for *S. ambigua* in 4 m² ($p < 0.05$) and 16 m² ($p < 0.05$) quadrats (Table 2). New juveniles were not included in these analyses. Juveniles mapped in 1984 that occurred in high density among conspecifics suffered significantly higher mortality than those that were relatively isolated. There was no association of juvenile mortality and local density of conspecifics for individuals of *S. ambigua* at the 2.25 m² scale nor for *A. dumosa* at the 16 m² spatial scale.

Mortality: Analysis b. The distribution of juveniles that died was significantly different from those that survived in *E. fasciculatum* ($p < 0.005$), and *S. ambigua* ($p < 0.05$) (Figure 1). For these species, juveniles that died occurred closer to adults. This analysis revealed no significant difference in juvenile survivorship of *A. dumosa* ($p = 0.843$) in relation to distance from the nearest adult.

(2) *Nearest neighbor distances.* A comparison of expected and observed nearest neighbor distances for the eight study species gives a first approximation of

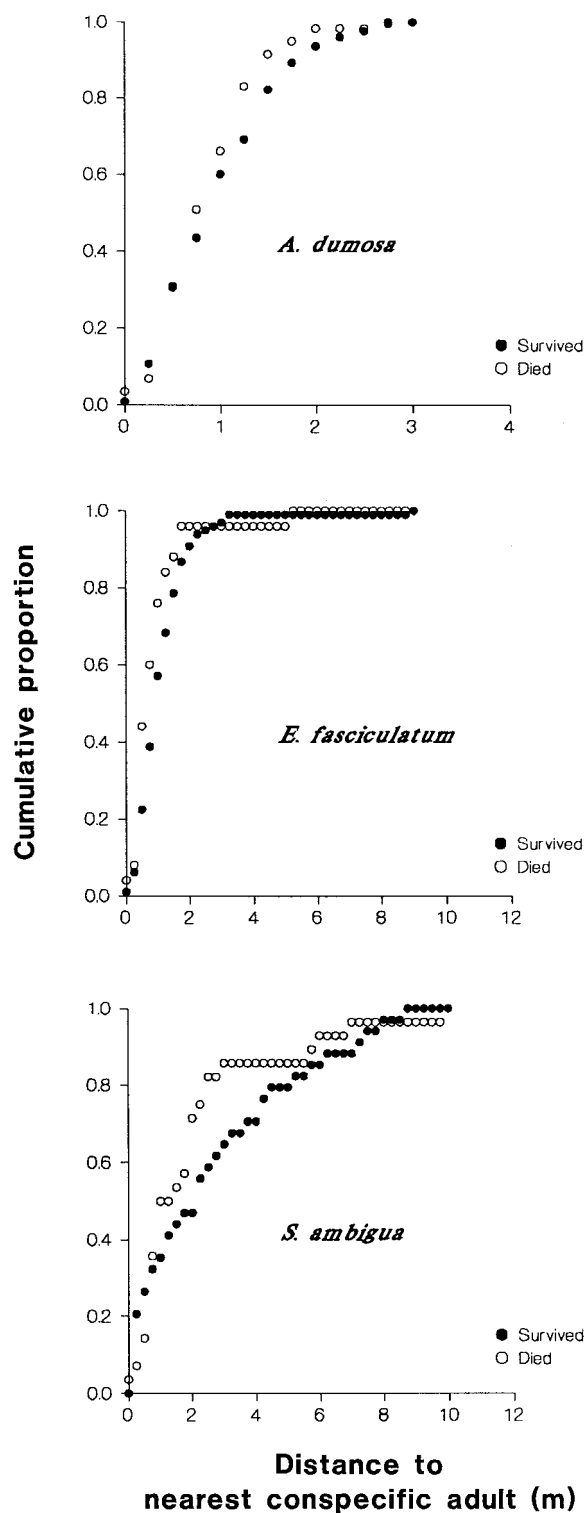


Figure 1. Relative distributions of juvenile plants from 1984 which survived (closed circles) or died (open circles). The cumulative proportion of surviving and dead plants is plotted as a function of distance from conspecific adults.

Table 2. Levels of significance for mortality analysis 1 which tests if the mortality of juveniles is dependent upon local density of conspecifics. P values < 0.05 indicate that there is a positive relation between local density of conspecifics in 1984 and juvenile mortality as of 1989 within the given quadrat size

Species	Quadrat size (m ²)	R^2	$P \leq$
<i>A. dumosa</i>	2.25	0.299	0.000
	4	0.452	0.000
	16	0.021	0.457
<i>S. ambigua</i>	2.25	0.199	0.096
	4	0.288	0.026
	16	0.343	0.017
<i>E. fasciculatum</i>	2.25	0.343	0.004
	4	0.638	0.000
	16	0.495	0.002

plant dispersion (Figure 2). Points located significantly below the expected line indicate aggregation, those above indicate hyperdispersion. Points which do not deviate significantly from the expected line lead to acceptance of the null hypothesis of random distribution. *Opuntia ramosissima* and *Yucca schidigera* show uniform patterns, while other species showed clumped or random patterns.

(3) *Juvenile and adult distribution.* Juvenile and adult distribution varied among species (Figure 3). Juveniles were dispersed randomly in relation to conspecific adults for *O. ramosissima* ($D_{\max} = 0.08$, $p > 0.10$), *S. chinensis* ($D_{\max} = -0.10$, $p > 0.10$), and *K. grayi* ($D_{\max} = 0.19$, $p = 0.10$). Juveniles were significantly aggregated near adults for *A. dumosa* ($D_{\max} = 0.35$, $p < 0.001$), *E. fasciculatum* ($D_{\max} = 0.75$, $p < 0.001$), and *S. ambigua* ($D_{\max} = 0.23$, $p < 0.005$). Juveniles were located farther away from adults than expected for *Y. schidigera* ($D_{\max} = -0.17$, $p < 0.05$).

(4) *Density.* Juvenile density was positively associated with adult density for *E. fasciculatum* ($p < 0.0005$), and *A. dumosa* ($p < 0.0005$). Density of juveniles was independent of adult density for *K. grayi*, *S. chinensis*, *O. ramosissima*, *Y. schidigera*, and *S. ambigua*.

(5) *Morisita's index.* Morisita's index indicated random distribution at all quadrat sizes for juveniles and adults of *Y. schidigera* and *S. chinensis*, adults of *O. ramosissima*, and adults of *A. dumosa*. Clumped patterns were found in juveniles and adults of *S. ambigua*, *K. grayi*, and *E. fasciculatum*, and for

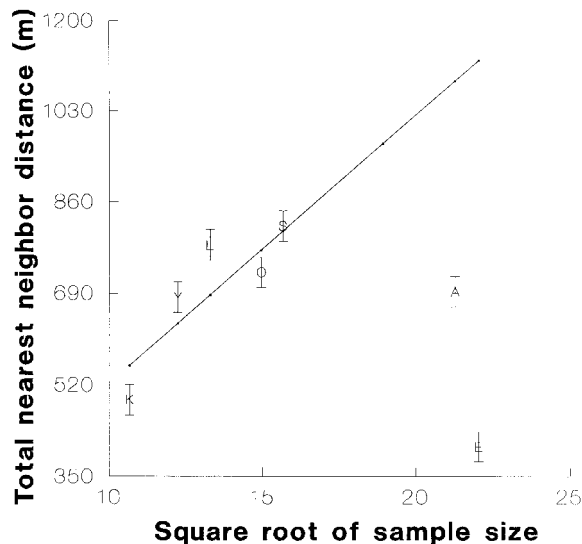


Figure 2. Dispersion as determined by conspecific nearest neighbor analysis. Points occurring significantly above or below the diagonal present uniform, or clumped patterns, respectively. The species represented on this graph are A = *Sphaeralcea ambigua*, E = *Eriogonum fasciculatum*, K = *Krameria grayi*, L = *Larrea tridentata*, O = *Opuntia ramosissima*, S = *Simmondsia chinensis*, Y = *Yucca schidigera*.

juveniles of *A. dumosa*, and *O. ramosissima*. The index is high for small quadrat sizes and decreases as quadrat size increases (Figure 4), indicating that clumps are randomly distributed within the study area.

Discussion

We evaluated the integrity of spatial pattern and patterns of mortality over five years for common perennial plants within a permanent one hectare study plot of mapped perennial shrubs. Spatial pattern has often been used to infer competitive interactions among plants, but multiple observations of a group of plants yields a more accurate account of plant dynamics. Spatial patterns of mortality strengthen inferences drawn from spatial pattern alone due to observation of differential mortality of near conspecifics.

Static spatial pattern

Different tests of dispersion measure varying aspects of pattern, offering different insights into negative interference among conspecifics. Nearest neighbor analyses measure the overall dispersion of individuals within the entire study area using the total number of individuals

within a given area. This test gives a first approximation of evidence of interference among conspecifics. A uniform distribution of conspecifics implies negative interactions among individuals. However these tests do not adequately address the degree of clumping at smaller quadrat sizes within a designated area. Morisita's index accomplishes this goal. The rate at which Morisita's index decreases towards unity with increasing quadrat size indicates the distribution of clumps within the overall study area. A decline in the value of the index shows that clumps are distributed randomly within the study area as was shown for juveniles of *A. dumosa* and *O. ramosissima*, and adults and juveniles of *E. fasciculatum* and *S. ambigua* (Figure 4). Comparison of juvenile to adult distributions (Hamill & Wright 1986) has the advantage of showing the degree of aggregation of juveniles around adults independent of overall intraspecific dispersion.

Independent of mortality and recruitment, intraspecific spatial patterns changed little from 1984 to 1989 (summarized in Table 3). Exceptions included that the degree of aggregation of juveniles no longer differed from that of adults for quadrats of 64 m² in *E. fasciculatum* and *S. ambigua*, and that there was a higher degree of aggregation among juveniles of *O. ramosissima* than was previously observed as evaluated by Morisita's index. Another difference included a nearest neighbor value showing a uniform rather than random pattern for *Y. schidigera*. The density of juveniles was no longer positively correlated to that of adults for *K. grayi*, and the juvenile to adult distribution for *Y. schidigera* changed from random to uniform.

These subtle differences in static spatial pattern may be attributable to the large number of juveniles establishing within the five year study period. With the exceptions of *S. ambigua* which showed high adult mortality, and *E. fasciculatum* which showed a large number of juveniles becoming adults, the number of adults within each species remained stable from 1984–1989. The study period included some years of low rainfall (Table 4), but mortality is not easily attributable to low water levels. High recruitment in several of the species and low mortality rates in others during the study period suggests that low precipitation did not have a large impact on the species, at least within the period discussed here. All species showed an increase in the number of juveniles represented within the study area (Table 1).

Overall, 'static analyses' of dispersion in the five-year census both confirmed and refined those made with the initial 1984 census (Wright & Howe 1987).

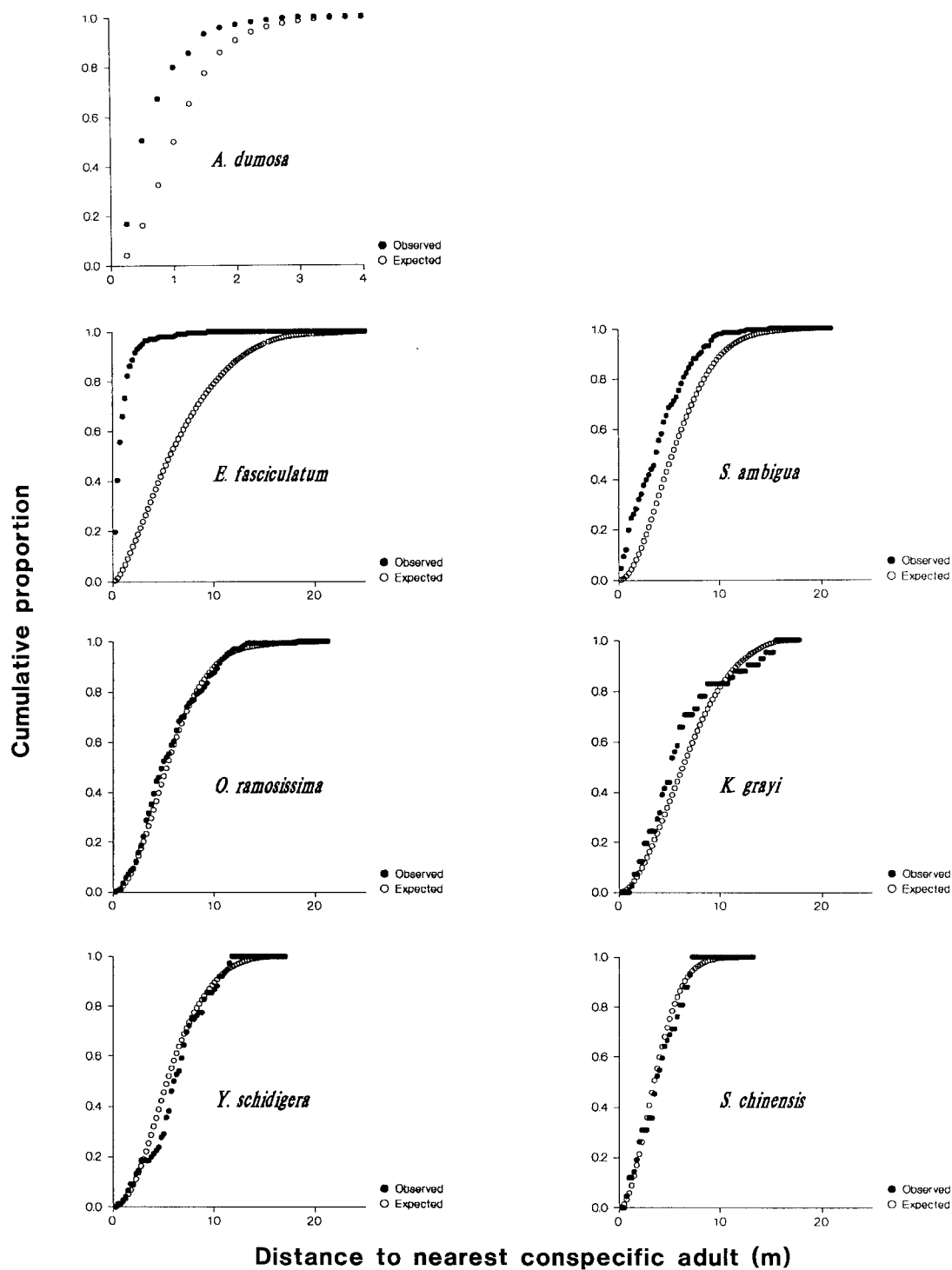


Figure 3. Relative dispersion of 1989 juvenile and adult plants. The cumulative proportion of juvenile (closed circles) and random points (open circles) are plotted as a function of distance from conspecific adults. Juvenile curves which are significantly above the random curve indicate that juveniles are aggregated around conspecific adults. Curves for *A. dumosa* only consider the first 750 m² of the study hectare.

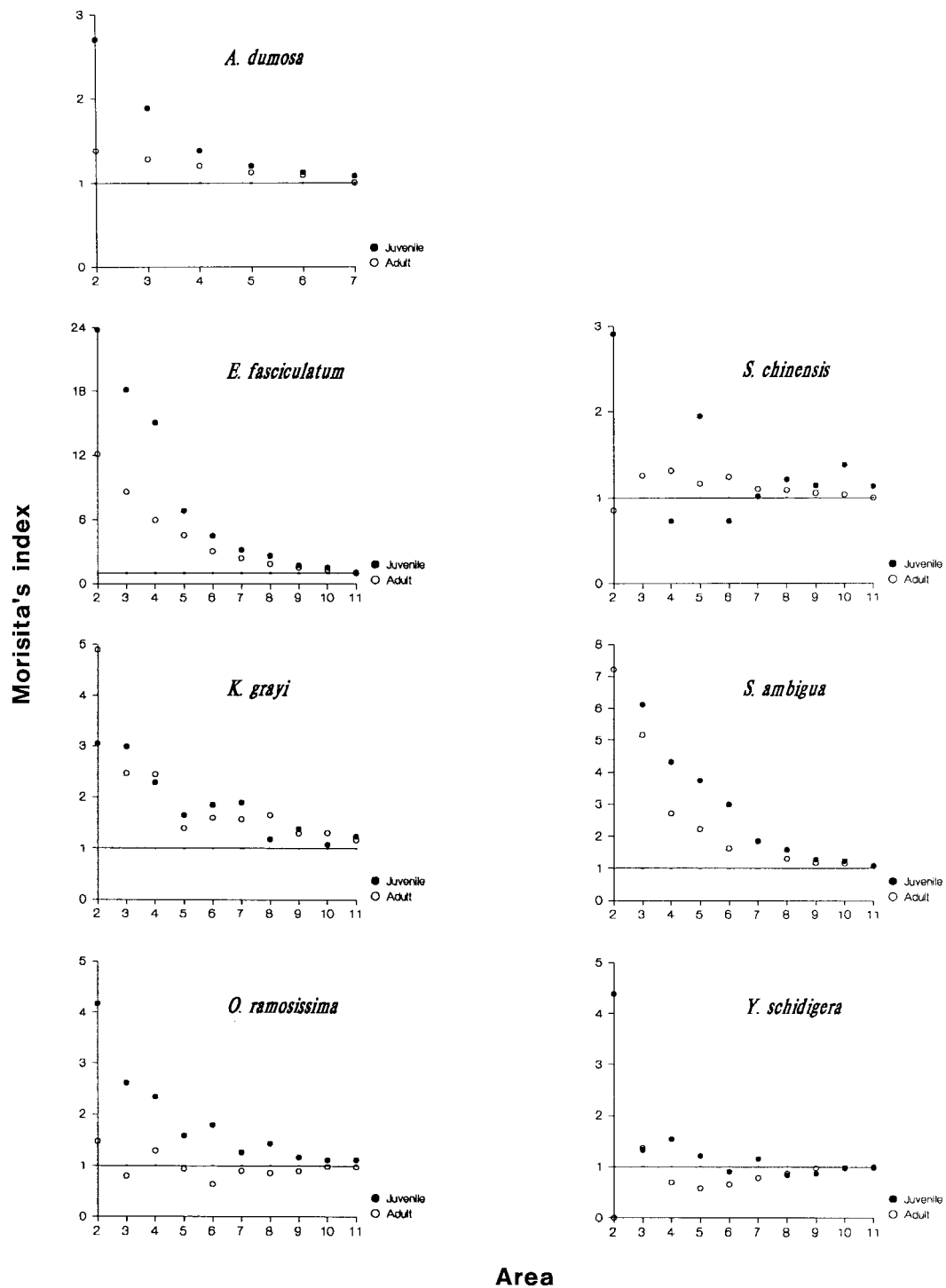


Figure 4. Morisita's index of dispersion for juvenile (closed circles) and adults (open circles). Points occurring significantly above the line $y = 1$, indicate aggregation for the spatial scale indicated on the x -axis; those occurring significantly below indicate hyperdispersion.

Table 3. Summary of spatial pattern analyses for species in which juveniles and adults can be distinguished

Species	Nearest neighbor distances ^a		Morisita's index ^b		Density of juveniles vs. adults ^c		Juvenile-adult distribution ^d	
	1984	1989	1984	1989	1984	1989	1984	1989
<i>Ambrosia dumosa</i>	C	C	J>A	J>A	P*	P***	C*	C***
<i>Eriogonum fasciculatum</i>	C	C	J>A	J~A	P***	P***	C***	C***
<i>Krameria grayi</i>	R	C	J~A	J~A	P**	NS	R	R
<i>Opuntia ramosissima</i>	U	U	J~A	J>A	NS	NS	R	R
<i>Sphaeralcea ambigua</i>	C	C	J>A	J~A	NS	NS	C***	C***
<i>Simmondsia chinensis</i>	R	R	J~A	J~A	NS	NS	R	R
<i>Yucca schidigera</i>	R	U	J~A	J~A	NS	NS	R	F*

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

^a C = clumped, R = random, U = uniform.

^b J>A = Morisita's index greater for juveniles than for adults, J~A = Morisita's index similar for juveniles and adults.

^c P = juvenile density positively associated with adult density, NS = no significant relation.

^d R = juveniles distributed randomly, C = juveniles aggregated about adults, F = juveniles located far from adults.

Uniform patterns of distribution, often used to infer competitive interactions among plants (Beals 1968; Woodell et al. 1969) remained rare among these desert plants. Common clumped and some random patterns of dispersion found in both analyses might leave the impression that intraspecific competition within these populations is unusual, although a shift from clumped juvenile to random adult dispersion for *A. dumosa* and *O. ramosissima* (Figure 4) suggests competition at early ages and stages. Changes in dispersion within populations between the 1984 and 1989 censuses show that static analyses of a single census cannot, by themselves, quantify pattern in desert plant populations. Mortality over five years offers the best complementary evidence that negative intraspecific interactions are important in *A. dumosa*, *E. fasciculatum*, and *S. ambigua*, three of the most abundant perennials at this site.

Patterns of mortality

Static pattern analyses cannot answer all questions about ecological processes. The role of biotic factors in determining spatial pattern would best be examined by accompanying patterns of recruitment and mortality over time. With few exceptions (e.g., Goldberg & Turner 1986), most studies of spatial pattern in deserts depend upon a single estimate based on static analyses. We recognize that census data do not distinguish mechanisms; the actual factors need to be evaluated

by experimentation. However, species interactions can generate characteristic patterns which can be seen in the dispersion of plants and in the spatial pattern of demographic processes. If negative plant-plant interactions are influencing the distribution of desert perennials, we can predict that either recruitment will be highest at greater distances from conspecifics, juvenile mortality will be highest within groups of clumped conspecifics, or juvenile survivorship will be highest beyond some critical distance from adults.

The ability to follow a cohort of plants over a five year time period revealed patterns of mortality that were not evident after a one year interval. Evidence of negative interactions was seen for *E. fasciculatum*, in which mortality was a positive function of conspecific density at all spatial scales tested (Table 2). Complementary to this result, a significantly high proportion of juveniles died when in close proximity (< 2m) to conspecific adults (Figure 1). These results, in addition to the observation that juveniles of this species are more highly aggregated than adults (Figure 4), suggest a thinning process consistent with the hypothesis that spatial pattern is a function of the size of individual plants (Greig-Smith & Chadwick 1965; Phillips & MacMahon 1981). The intensity of competition is expected to increase as plants increase in size, eventually leading to competitive exclusion of near neighbors. Although such competitive exclusion may be occurring in *E. fasciculatum*, it still presents a clumped distribution. In general, long-lived species may allow for a

Table 4. Annual rainfall from 1970–1989

Year	Annual precipitation (cm)
1970	8.3566
1971	10.0076
1972	1.8796
1973	3.9370
1974	7.1882
1975	7.6200
1976	16.8910
1977	26.8478
1978	25.3746
1979	16.3068
1980	18.2626
1981	7.4676
1982	16.8656
1983	31.2928
1984	17.1704
1985	11.3030
1986	8.6360
1987	11.9126
1988	3.3020
1989	4.2164

regular pattern to develop based on low establishment of seedlings and a slow thinning process, while shorter-lived species may never complete the thinning process (McAuliffe 1988).

Evidence of negative interactions was not as apparent for *A. dumosa* and *S. ambigua*. Regression analyses for *A. dumosa* indicate that juvenile mortality is a positive function of conspecific density at smaller quadrat sizes, suggesting density dependent mortality. However, the lack of differential mortality of juveniles as a function of distance to conspecific adults does not support negative plant-plant interactions. It has been suggested that *A. dumosa* has the ability to establish in open habitat (McAuliffe 1988) and this, too, has been observed within our study site. Mortality among clumped juveniles away from adults may be caused by different factors than mortality among those located near adults and our tests do not address this difference. Herbivores may preferentially forage away from an adult canopy in some situations (McAuliffe 1986; McAuliffe 1990) or near an adult canopy in others (Brown et al. 1988; Brown 1989). Such behavioral differences among plant predators confound analyses of patterns of mortality among conspecifics and can not be readily addressed by our study.

Juvenile mortality increased with density for the larger two quadrat sizes examined in *S. ambigua* ($p < 0.05$, Table 2). There was a significant difference in juvenile survivorship and mortality curves as a function of distance from conspecific adults. Of the juveniles that died, the greatest proportion of juvenile deaths occurred at distances from 1–3 m from conspecific adults, which would not place them immediately underneath adult canopies for this species at this site (M. Miriti, unpublished data). At distances of less than one meter, proportionally more juveniles survived. As above, adults may offer protection for juveniles located immediately underneath their canopy (< 1 m distance), leaving juveniles at greater distances exposed to herbivory and/or desiccation.

E. fasciculatum, *A. dumosa* and *S. ambigua* all showed clumped patterns of distribution as adults, and the reevaluation of pattern over the five year study shows no evidence that this pattern is changing. Although some disproportionate mortality exists among conspecific juveniles, the thinning process, if it occurs, is slow. In addition, *E. fasciculatum* and *A. dumosa* show 80% of surviving juveniles within a distance of 2 m from conspecific adults (Figure 1), while the same percentage survivorship occurs for juveniles within 4 m from conspecific adults for *S. ambigua*. The range of distances for high juvenile survivorship is the same as that for high juvenile mortality. Nevertheless, juveniles of these three species are located closer to adults than would be expected by chance (Figure 3) implying that competition among these juveniles may be relatively more important than any negative effects of adults.

This first dynamic data set offers some interesting insights into the distribution and abundance of desert perennial plants. In general, conspecific spatial patterns changed little over five years. Mortality over one year yielded little evidence of intraspecific interference among the species tested, but analysis over five years does suggest competitive interactions within at least one species (*E. fasciculatum*).

Heterospecific interactions are also likely to affect overall plant distribution in contrasting ways. Preliminary analyses of heterospecific juveniles around *A. dumosa* adults within the first 750 m² of the study hectare indicate that for many species, juveniles are more strongly aggregated around adults of this species than around their own conspecific adults (unpublished data), suggesting potential nurse effects (see Turner et al. 1966; 1969; Franco & Nobel 1989). Long-lived species may asymmetrically limit the distribution of

shorter lived species. Herbivores and granivores may more strongly influence spatial pattern (e.g., McAuliffe 1986; Inouye et al. 1980) than plant-plant interactions. Such interactions need to be evaluated experimentally. These results have been used to design experiments which will measure the effects of herbivores, granivores and nurse plants on the dispersion of desert plants.

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