

Henry F. Howe and S. Joseph Wright

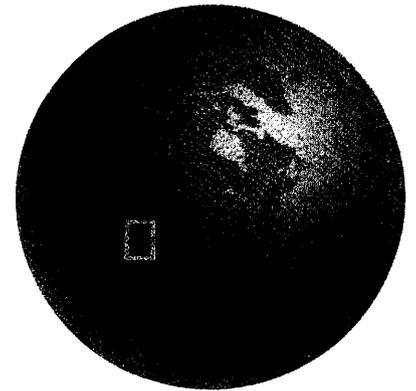
Spatial Pattern and Mortality in the Desert Mallow (*Sphaeralcea ambigua*)

The authors mapped the perennial desert mallow (*Sphaeralcea ambigua*) in a hectare of the Mojave Desert and followed survivorship for one year. Deaths occurred independently of the locations of other individuals of the same species or other species. Correlations occur between the sizes and distances of numerically dominant and long-lived species, such as creosote (*Larrea tridentata*) and burroweed (*Ambrosia dumosa*), but such correlations do not occur in the smaller and short-lived mallows. These and other small perennials are fugitive features of the desert landscape, occupying suitable spots where their shallow roots stake a temporary claim.

For a plant at the edge of the desert is said to struggle for life against the drought, though more properly it should be said to be dependent on the moisture (Darwin 1859:62).

Deserts are communities of sparse vegetation and physical extremes, characterized by annual rainfall of < 200 mm, potential evapotranspiration of > 2000 mm, and wide swings in surface temperatures (Walter 1985). Biophysical properties actually vary a great deal. By comparison with the stark central Sahara, which receives < 100 mm of rain and has > 5000 mm of potential evapotranspiration, arid lands of the southwestern United States appear well-watered and benign. What all of these arid lands have in common, however, is a climate of harsh extremes that subjects their inhabitants to virtually constant desiccation, freezing winters, and midsummer hardpan temperatures exceeding 60°C. Even at their most productive extremes, deserts show sparse vegetation interrupted by considerable stretches of bare ground, shrubs or cacti rarely taller than 3 m, and deciduous, cutinized, or succulent stems and leaves that attest to a constant "struggle for life against the drought."

Spatial patterns of desert plants are of interest because they should reflect the extreme manifestations of competition for a limited resource: water. Apparently regular distributions of some species, such as creosote (*Larrea tridentata*), are variously interpreted as consequences of direct competition for water or allelopathy (MacMahon & Schimpf 1981, Sheps 1973). In some cases experimental removal of perennials has in fact shown that desert plants reduce the xylem water potentials, growth rates, and reproductive outputs of adult neighbors (Ehleringer 1984, Fonteyn & Mahall 1978, Robberecht et al. 1983) or of nearby seedlings (Friedman 1971, Sheps 1973). The general barrenness of the landscape, and the results of distributional or experimental studies for a few

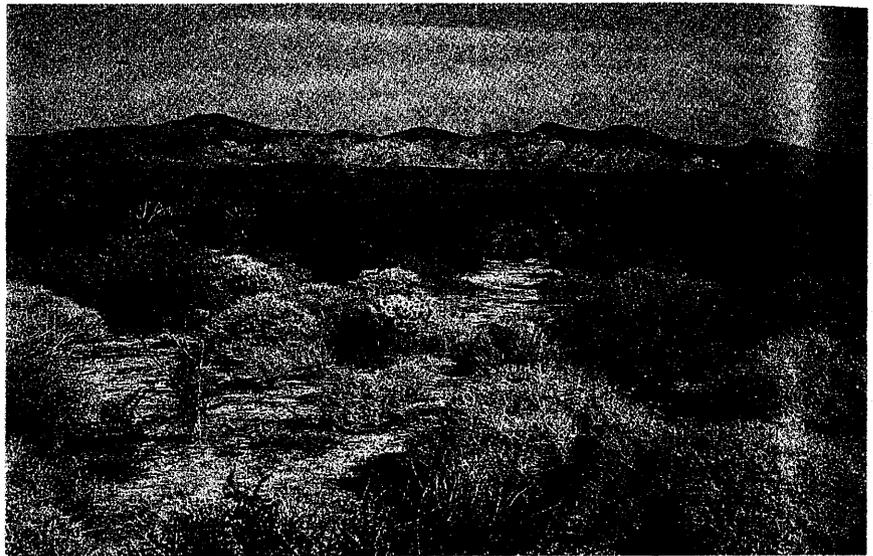


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plant species, suggest that "negative interference" (sensu Harper 1977) from direct competition for water or allelopathy is of widespread significance in desert communities.

At the same time, countervailing evidence complicates the issue of pervasive negative interference. Desert shrubs often are statistically aggregated (Anderson 1971, Barbour 1973), and frequently grow in interspecific clumps (Figure 1). In fact, a generalization as venerable in the desert literature as competition forcing spatial dispersion is the assertion that many perennials only establish as seedlings under the shade and mechanical protection of larger "nurse plants" of the same or different species (Muller 1953). In at least one confirmed case involving the saguaro cactus (*Carnegiea gigantea*) in the Sonoran Desert of the United States, seedlings without nurse shrubs are virtually always killed by desiccation or rabbit herbivory (Steenbergh & Lowe 1977). Even plants of

Figure 1. The Mojave Desert study area is a gently sloping bajada, or outwash plain, at the base of the Eagle Mountains in Joshua Tree National Monument. At an altitude of 1000 m, this is a desert landscape of widely scattered shrubs such as burrowweed (*Ambrosia dumosa*), creosote (*Larrea tridentata*), and Mojave spurge (*Tetradlopus hallii*), intermixed with smaller numbers of pencil cholla (*Opuntia ramosissima*) and silver cholla (*Opuntia echinocarpa*).



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arid landscapes can benefit from each other's presence.

The authors tested the alternative hypotheses of negative interference and nurse plant protection, against the null hypothesis of random mortality, for the desert mallow (*Sphaeralcea* Gray spp. *ambigua*; Malvaceae), a short-lived perennial of the Colorado and Mojave Deserts of southern California and Mexico (Figure 2). Field tests used spatial dispersion and annual mortality in a cohort of 290 plants in a hectare of Mojave Desert in southern California to address the following questions:

- Does spatial dispersion suggest negative interference, the nurse effect, or random spacing? A likely statistical result of competition would be hyperdispersion, or spacing. On the other hand, juveniles clumped around adults might represent cohorts of offspring around parents, or even a nurse effect resulting from protection of vulnerable young plants by the shade of older ones.
- Are plants near neighbors more or less likely to die than those farther away? Competition should result in higher mortality of mallows near other plants of the same or different species, while the nurse effect should enhance survival of plants near neighbors.
- Are juvenile plants more influenced by the proximity of neighbors than old plants? Negative interference should result in higher mortality of young plants near more dominant individuals of the same or different species, while the nurse effect might be expected to enhance the survival of young plants near larger ones. This third hypothesis is important be-

cause nurse effects are most likely to favor small plants most vulnerable to desiccation or herbivory; the same individuals might become competitive with nurses as they develop mature root systems and canopies.

This paper considers mortality of one of 24 species of woody perennials growing on the study area. Because of its relatively short lifespan, desert mallow yields substantial demographic information after only one year. The objective here is to analyze the distribution and local abundance of this common perennial of the Mojave Desert, using an approach that integrates traditional measures of static pattern and cohort survivorship, as well as a novel measure of juvenile and adult spatial relations. Such an integrated approach offers a unique level of resolution to inferences that, when based on only one method (e.g., a measure of static pattern), are inherently ambiguous. (The authors' discussions of other species are forthcoming.)



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Study Site

The study site is on a bajada (elevation, 1006 m) that slopes to the northwest of the Eagle Mountains in Joshua Tree National Monument (Figure 1) (long $115^{\circ}47'$, lat $33^{\circ}46'$). Rainfall averaged 18.6 cm/yr, 2 km away at the Cottonwood Spring ranger station between 1970 and 1984. This site is dominated by burroweed (*Ambrosia dumosa*; 70% of the stems), but other conspicuous plants among the 24 perennial species present include creosote (*L. tridentata*).

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

Figure 2. Desert mallow (*Sphaeralcea ambigua*): left, a mature plant; right, a partially open flower in characteristic daytime pose.

Methods

Plants ≥ 10 cm tall were mapped to the nearest 0.25 m in a 1-ha block between 15 March and 8 April 1984. Survivorship was documented after one year (23 March to 3 April 1985). Each plant was marked with a numbered aluminum tag.

Plants were divided into two age classes on the basis of volume and reproductive history. Following Phillips & MacMahon (1981), volume (V) was calculated as if plants were oblate spheroids so that

$$V = \frac{\pi a^2 b}{6} \quad (1)$$

where a is the smaller and b the larger of the height and the average of the major and minor axes, measured in 1984.

Reproductive status for most individuals was obvious from flower buds, mature flowers, and old inflorescences. The relationship between the proportion of individuals that had such structures and plant volume approximates a sigmoid curve; the inflection point of the sigmoid curve establishes a cutoff volume that separates nonreproductive or juvenile plants from reproductive or adult plants (Figure 3).

Spatial Pattern

Six analyses of static spatial pattern were performed. Several of the analyses are at least partially redundant. Nevertheless, multiple analyses are desirable because the choice of analysis can affect results (e.g., Phillips & MacMahon 1981:Table 3).

(1) Donnelly (1978) provides expected values and variances of total nearest neighbor distances (TNND) under the null hypothesis that plant locations are indistinguishable from a random distribution. A standard normal deviate tests the null hypothesis.

(2) Morisita's (1959) index estimates dispersion from counts of individuals among quadrats of area, 2^xm^2 , where x takes all integer values between 2 and 11. Morisita's index is:

$$I = q \sum_{i=1}^q n_i (n_i - 1) / N(N-1) \quad (2)$$

where q is the number of quadrats, n_i is the number of individuals in quadrat i , and $N = \sum n_i$. The index equals 1 under the null hypothesis (see analysis 1 above), is > 1 for aggregated patterns, and is < 1 for regular patterns. An F-test and 64- m^2 quadrats were used to evaluate the null hypothesis (Morisita 1959).

Morisita's index was calculated separately for juveniles and adults. While this may indicate that the dispersions of juveniles and adults differ, no insight is provided into the relative positions of juveniles and adults. For example, if juveniles are aggregated, they may be found primarily in the interstices among adults, at the bases of adults, or independently of adults. These are all reasonable alternatives (Hamill & Wright 1986); therefore, how are juveniles distributed relative to adults?

(3) The null hypothesis that densities of juveniles and adults were independent was tested. The mapped hectare was divided into 16 subplots of 625 m^2 each and the number of juveniles in each subplot was regressed against the number of adults.

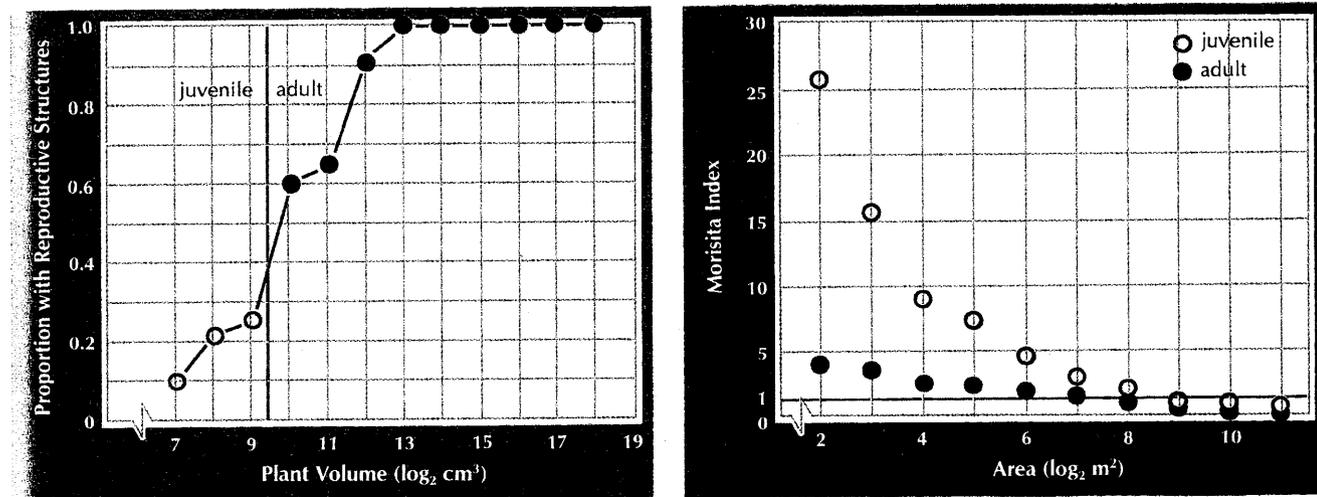
(4) A test proposed by Hamill & Wright (1986) was used to examine the relative dispersion of juveniles and adults. This test compares observed and expected distances between juveniles and nearest conspecific adults. Let D_k represent the distance between juvenile k and the

nearest conspecific adult. For any distance d , define $F_0(d)$, the observed probability that $D_k \leq d$ as

$$F_0(d) = \frac{\sum_{k=1}^J I_k}{J} \quad (3)$$

where J is the number of juveniles and I_k is an indicator variable that equals 1 if $D_k \leq d$, and 0 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 plants were mapped to the nearest 0.25 m, x and y take all values between 0 and 100 that are multiples of 0.25,



giving 401^2 possible locations. Now,

$$F_E(d) = \sum_{y=0,0.25}^{100} \sum_{x=0,0.25}^{100} I_{x,y} / 401^2 \quad (4)$$

where $I_{x,y} = 1$ if $D_{x,y} \leq d$ and 0 otherwise. Note that $F_0(d)$ and $F_E(d)$ are probability density functions. $F_0(d)$ and $F_E(d)$ were calculated from the 1984 map and a two-tailed, one-sample Komolgorov-Smirnov test was used to compare the distributions. Hamill & Wright (1986) discuss this test more fully and demonstrate its usefulness against a variety of non-random distributions.

(5) Pielou (1960) first suggested that negative interference might cause a positive relationship between the summed volumes and distances between neighboring plants. The null hypothesis that the summed volumes and distances between nearest conspecifics were independent was tested. To ensure 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.

(6) The hypothesis that mallows are more likely to die near large than small neighbors was tested in both intraspecific and interspecific comparisons. Under negative interference, mortality should be positively correlated with neighbor volume. A strong nurse effect should produce a negative correlation between mallow mortality and neighbor volume.

Figure 3. Reproductive status as a function of plant volume. Reproductive status is plotted on the ordinate as the proportion of individuals in each volume category that bears reproductive structures. The gray line indicates the volume used to separate juveniles from adults. Analyses of dispersion based on quadrat counts for adult and juvenile desert mallows (*Sphaeralcea ambigua*). The index equals 1 when plants are distributed at random, and takes values greater and less than 1 for aggregated and regularly dispersed individuals, respectively.

Results

Between 1984 and 1985, 25.4% mortality was recorded for *S. ambigua*. With an initial sample of 217 adults and 73 juveniles, enough data exist to test each hypothesis of interest.

(1) *S. ambigua* is highly aggregated in space, showing a standard normal deviate of 8.3 (Table 1) (Donnelly 1978).

(2) When juveniles and adults are analyzed separately with Morisita's index, *S. ambigua* juveniles and adults are both aggregated, and juveniles are more aggregated than adults (Figure 4). The decline in Morisita's index with increasing quadrat size is characteristic of those populations in which individuals occur in clumps, and the dispersion of individuals within clumps is random (Morisita 1959). In general, how-

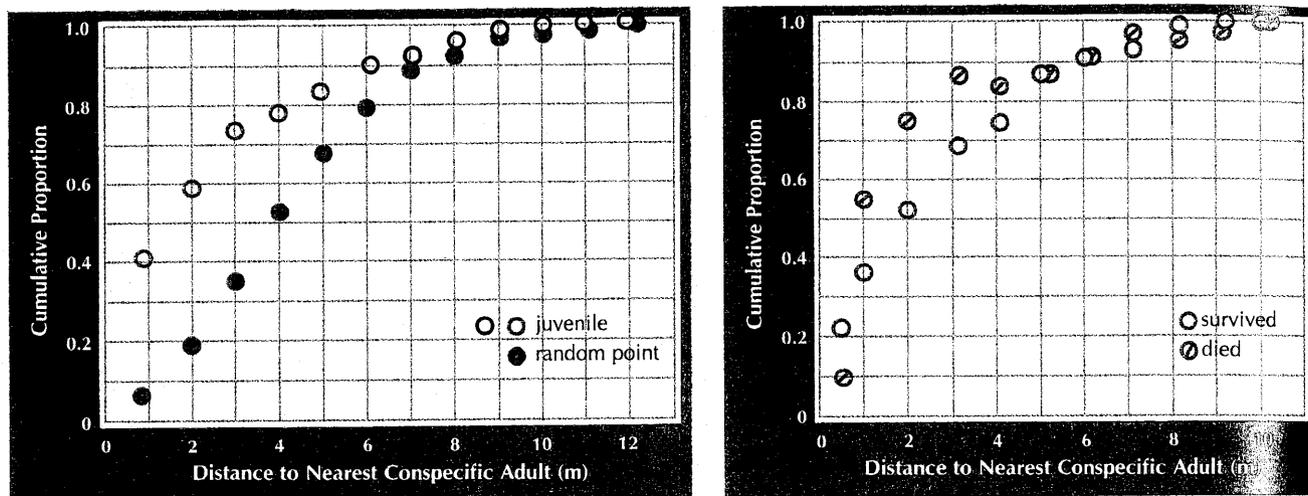


Figure 5. Relative dispersion of adult and juvenile desert mallows. The cumulative proportions of juveniles and random points are plotted against distance. Red circles indicate values significantly different from those predicted by a null distribution. Juveniles are invariably found closer to conspecific adults than expected by chance. 6. Mortality and survivorship of juveniles as a function of distance to the nearest conspecific adult. Cumulative proportions of juveniles that died and that survived are plotted against distance. Isolation does not affect survivorship significantly.

ever, nearest neighbor and quadrat analyses gave similar results for the desert mallow.

(3) Numbers of juveniles and adults in 625-m² subplots were neither positively nor negatively correlated (Table 1).

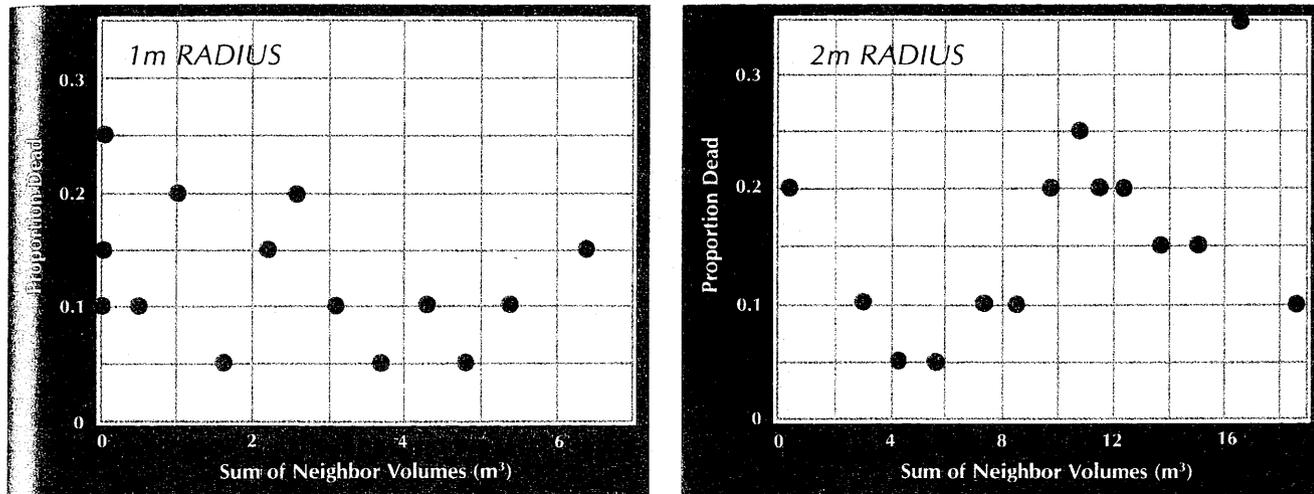
(4) The null hypothesis that juveniles are distributed independently and randomly with respect to adults was rejected ($p < 0.001$). Juvenile-adult distances are consistently shorter than expected (Figure 5).

(5) The summed volumes and distances between nearest neighbors were not correlated ($p > 0.14$). Large neighbors in this community are no more likely to be associated with small desert mallow plants than with other large plants.

(6) Mortality of juvenile *S. ambigua* provides no evidence for negative interference from conspecifics or heterospecifics. The proportion of individuals that died was independent of the initial density of conspecifics ($p > 0.10$) at all spatial scales tested. Distance to the nearest conspecific adult did not differ for juveniles that survived and juveniles that died ($p > 0.10$) (Figure 6). Nor was mortality of *S. ambigua* correlated with the sizes (volumes) of neighbors within a 1- or 2-m radius (Figure 7). Analyses at 0.2-m intervals between 0.2 and 2 m have similarly negative results. Interspecific analyses also fail to suggest negative interference; the frequency of death was similar for juveniles that were initially isolated from all other plants and for juveniles that were in physical contact with another plant ($\chi^2 = 1.09, p > 0.10$) (Table 2). These mortality data show neither an advantage nor a disadvantage to proximity of neighbors of different sizes for the desert mallow.

Discussion

Harsh ecological extremes may influence plant mortality, and consequently the spatial dispersion of plants, in a variety of ways. Conditions may be so extreme that plants die randomly with respect to others of their own or different species. This is common for seeds of Old World deserts (Ellner & Shmida 1981), and might be expected in seedlings, juveniles, or small adults with root systems too small to be in direct contact with those of potential competitors. If mortality is random, establishment determines spatial pattern. The population may be highly aggregated if juveniles are more likely to establish near parents than elsewhere. Alternatively, competition may promote predictable patterns of mortality and spatial dispersion. Plants close together may suffer



more than those far apart, and large plants may successfully exclude smaller competitors from their immediate vicinity. Strong competition resulting in density-dependent interference should produce more or less regular distributions, producing spaced patterns of adult plants so familiar in desert lore. Finally, nurse plants protect juveniles from desiccation or herbivory and should, if the nurse effect is strong, promote aggregations of juveniles of species other than their own. The nurse effect, if present, should disappear as juveniles reach sizes that are competitive with their nurse plants.

An analysis of spatial pattern alone more often than not gives ambiguous results (Anderson 1971, Barbour 1973). Competition may produce spacing among adults, but recruitment of seedlings near parents may still produce aggregations of plants of mixed ages. Moreover, different methods yield different results. A heterogeneous habitat may include spaced populations within patches of especially suitable edaphic conditions, and few or no individuals elsewhere. A quadrat analysis with small blocks might easily produce statistical regularity if the entire study area is encompassed by suitable edaphic conditions, but produce statistical aggregation if blocks include both suitable and unsuitable edaphic conditions. It is now acknowledged that either direct experiments or analysis of patterns of establishment and mortality must accompany analyses of spatial pattern in order to tease apart the relative influences of negative interference, the nurse effect, or random mortality for any given species of desert perennial (Fonteyn & Mahall 1981, Wright 1982). If only measurements of aggregation or hyperdispersion are taken into ac-

Figure 7. Mortality of desert mallow (*Sphaeralcea ambigua*) as a function of the size of shrub neighbors within 1 and 2 m. The proportion that dies is independent of the total volume of neighbors within 1-m radii ($r = 0.35$, $p > 0.2$) or 2-m radii ($r = 0.40$, $p > 0.1$). In short, having a near neighbor is neither a significant advantage nor a significant disadvantage in this sample.

Table 1. Summary of Dispersion and Mortality Data for Desert Mallow*

Test	Result	p
ALL INDIVIDUALS		
Nearest neighbor	aggregated	≤ 0.001
Quadrat counts	aggregated	≤ 0.01
JUVENILES COMPARED WITH ADULTS		
Nearest neighbor	juveniles aggregated around adults	≤ 0.001
Quadrat counts	juveniles more aggregated than adults	N/A [†]
Correlation of densities		NS

*Morisita's Index numerically greater for juveniles than for adults

[†]Significance tests not available

Table 2. Mortality of Desert Mallow Juveniles as a Consequence of Physical Contact with Other Plants

	Alive	Dead
Solitary	20	10
Contact conspecific	1	0
Contact heterospecific	32	8

count, they can be attributed to a variety of ecological phenomena.

The present study of dispersion and mortality of the desert mallow offers unique insights into the ecology of small desert perennials that must coexist with adults of much larger and more established species. In the extreme example, clones of the much larger shrub creosote (*L. tridentata*) have been aged at over 12 000 years (Vasek 1980); individuals of this species on the study area are large enough to have been present for 1500 to 2000 years. Ages of burroweed (*A. dumosa*), which accounts for 70% of the individual plants on this plot, have not been determined, but abundant large individuals are likely to be at least 50 to 100 years old. How can a small, short-lived shrub survive in a barren, resource-limited world occupied by such formidable neighbors?

Desert mallow is apparently a fugitive plant in its own home, occupying the narrow interstices between larger shrubs, where it establishes, flourishes, and dies with little noticeable interaction with its neighbors. There is no evidence of negative interference in this species. Large plants do not interfere with smaller conspecifics, nor is there any sign that close neighbors suffer more than widely scattered individuals. In fact, the only statistically significant correlation between size (shrub volume) and distance to neighbors in the study area has been found to occur in the two large dominant shrubs (creosote and burroweed), which are long-lived enough to have established consistent competitive interactions among individuals (Wright & Howe in preparation). The absence of negative interference so obvious in the desert mallow may generally apply to small species of the Mojave community.

Do desert mallows establish under the protection of nurse species? Mallows often grow in contact with other plants (Table 2), but there is no evidence that they achieve any significant benefit from these associations. Unlike saguaro cactus (*C. gigantea*) seedlings, which must establish under a nurse bush to avoid desiccation and herbivory by jack-rabbits (Steenbergh & Lowe 1977), desert mallows are just as likely to die under a nurse plant as in the open. The nurse hypothesis must be rejected as decisively as the negative interference hypothesis.

In short, the authors find that desert mallow spatial dispersion and demography appear to be representative of patterns likely to occur in a wide variety of small shrubs forced to coexist with larger species that are, from their perspective, permanent and potentially lethal competitors for limited water. Abundant seeds, small size, shallow root systems, and short lives should characterize these plants, which until now have been virtually ignored among the venerable giants and ephemeral annuals of arid-land communities. Whereas isolated analyses of static spatial pattern or short-term demography virtually always gives ambiguous results, an integrated analysis of *S. ambigua* unambiguously points to the relevance of random mortality in desert communities.

Acknowledgments

We thank Robert Moon, Wes 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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Accepted 19 June 1986.