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DISTRIBUTIONAL ASSOCIATES OF THE SAGUARO (*CARNEGIEA GIGANTEA*)

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ABSTRACT—The spatial distribution of the saguaro (*Carnegiea gigantea*) was studied with respect to its occurrence in open space or space covered by various perennial plant species at Organ Pipe Cactus National Monument, Arizona. Saguaros occurred significantly less often than expected in the open and significantly more often than expected under the canopies of perennial plants. Saguaros were associated with other species about as often as expected on the basis of their relative cover values, with two exceptions. They were found growing in association with *Larrea tridentata* significantly less often than expected, and with *Prosopis juliflora* and *Cercidium microphyllum* more often than expected. The degree of association with the varius perennial plant species did not change with age of the saguaro for saguaros exceeding about 19 years of age (10 cm in height). Abundance of saguaro seeds was recorded from directly beneath the canopy of *C. microphyllum*, at the edge of its canopy, and one m out from the canopy. Seed densities decreased significantly with distance from the base of the nurse tree. Such nonrandom seed dispersion resulting from differential seed predation or differential seed dispersal is a potentially important factor contributing to the dispersion patterns of adult saguaros.

One of the most conspicuous patterns of plant distribution in the Sonoran Desert is that represented by the saguaro (*Carnegiea gigantea*). As long ago as 1859, Engelmann noted that young saguaros " . . .are almost always found under the protecting shade of some shrub, especially 'green-barked acacia' (*Cercidium floridanum*) so characteristic of the barren wilderness, and not rarely the dead stems of this plant [the acacia] are found near the older cerei." In each of several subsequent publications (Shreve, 1931a; 1931b; Niering et al., 1963; Turner et al., 1966) similar observations were recorded.

Surprisingly, the assumed nonrandom distribution pattern of saguaros was never established quantitatively. In the only existing study of the distributional associates of saguaros, McDonough (1963) concluded that "significant positive associations were not found between any pair of species at all three quadrat sizes used, a requirement for the tentative estasblishment of a biotic effect ..." and that "... the associations between *Carnegiea-Cercidium* are no more than suggestive of the possible contribution made by the cover of this species to the establishment of the cactus ..." However, McDonough's conclusions were based, in part, on data collected from quadrat sizes that would be insensitive to biological interactions that occur on a small spatial scale, and on data that did not allow a comparison of the availability of space to its use.

There are no published studies that quantify the relative degree of association between saguaros and the various species that might serve as nurse plants. Since the point at which saguaros become independent of nurse plants is unknown, but possibly as soon as 5-10 years, while still only 2 cm tall (Turner et al., 1966), one would assume that the benefits derived from a nurse plant could be provided equally well by most any perennial plant species, and that saguaros ought to occur in association with other species about as frequently as would be expected on the basis of the relative cover provided by each. Steenbergh and Lowe (1969) suggested that this might be the case for *Cercidium microphyllum* and *Encelia farinosa*—two common perennial species in their study plots.

In this paper the distribution of *Carnegiea gigantea* is examined relative to available space. Associations with various plant species are evaluated, and changes in the distributional associates between early and later stages of life are examined. Information is also provided concerning the abundance of saguaro seeds to determine the presence of an initial bias in the distribution of seeds that would contribute to a nonrandom distribution pattern of adults.

STUDY SITE—Two study sites were located in Organ Pipe Cactus National Monument, Arizona. Site 1 was located on the lower bajada, 6 km southwest of the monument headquarters (31°55'N, 112°50'W) and was dominated by *Larrea tridentata* and *Ambrosia deltoidea*. Site 2 was located in an area of rocky-scoriaceous, basaltic soils, 3 km north of monument headquarters (31°58'N, 112°47'W) where *L. tridentata, A. deltoidea*, and *Cercidium microphyllum* each provided about 25% of the total plant cover.

METHODS—Data were collected from 19-29 March 1981 and 19-28 March 1982. Scientific nomenclature for all plant species follows Shreve and Wiggins (1964). Twenty parallel 100 m transects were located at site 1 and 5 at site 2. Transects were spaced approximately 50 m apart. Cover was estimated by determining species of perennial plant, if any was present, beneath the tip of a 2 m rod held first to the right then to the left, perpendicular to the transect at 1 m intervals.

The height of every saguaro and the height and species of each associate that occurred within 5 m of either side of the transect was determined. Associates were perennial plant species whose canopy included the base of the saguaro. An additional measurement at the second site was the number of other saguaros growing within 2.5 m of the subject saguaro. The latter measurement was used to determine the degree of clumping under various growth conditions.

In order to assess the abundance of saguaro seeds at varying distances from the base of a potential nurse tree, soil samples were collected from beneath six *Cercidium microphyllum* trees that were located on the slopes and flats. The sample trees were isolated from saguaros by at least 10 m. Forty-eight samples (10 cm in diameter by 2 cm deep) were collected beneath each tree, with 16 samples spaced equidistantly in a circle midway between the canopy edge and the bole, 16 under the canopy edge,and 16 1 m beyond the canopy edge. Saguaro seeds were identified on the basis of the size and shape characteristics presented in Engelmann (1859) and Steenberg and Lowe (1977). The seeds were extracted from the soil by lightly pulverizing each sample and straining the floating vegetative material from the surface of a tub of water.

Statistical methods included G-tests to determine the significance of differences between observed and expected frequency distributions, chi square tests on data subjected to contingency table analysis, and a one-way ANOVA to determine the significance of differences among means (Sokal and Rohlf, 1981).

RESULTS—At both the lower bajada site and the rocky basalt site, the open area between plant canopies accounted for about 60% of the available space, with *Larrea tridentata* and *Ambrosia deltoidea* having 20-30% cover (Fig. 1 A, C). Saguaros occurred beneath perennial plant species significantly more often, and in open areas significantly less often than expected due to chance ($G = 217$ and 264; $P < 0.001$ for sites 1 and 2, respectively) (Fig. 1 A, C).

Considering only those saguaros growing with associates, they were distributed nonrandomly among the possible associate species at each site

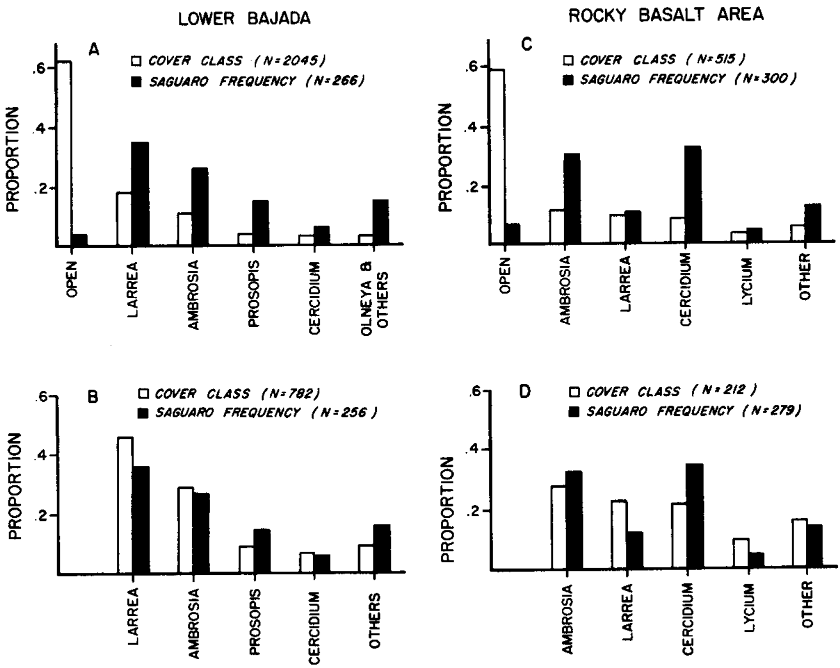

FIG. 1—The relative frequency distribution of available space (cover class) and the relative frequency of conditions where saguaros were observed growing (A, C). The relative cover of each of several associate species and the relative frequency of co-occurrence with saguaros (B, D).

($G = 18.1$ and 20.0; $P < 0.01$ for sites 1 and 2, respectively). Specifically, saguaros were observed more often with *Prosopis juliflora* ($G = 7.2$, $P < 0.01$) and less often with *Larrea tridentata* ($G = 7.7$, $P < 0.01$) than expected at site 1, and were observed more often with *Cercidium microphyllum* ($G = 9.9$, $P < 0.01$) and less often with *L. tridentata* ($G = 10.1$, $P < 0.01$) than expected at site 2 (Fig. 1 B, D). All other associates occurred no more or less frequently with saguaros than expected on the basis of their relative cover values.

The mean number of additional saguaros growing within 2.5 m of the subject saguaro was much greater for the large tree-like *Cercidium microphyllum* and *Olneya tesota* than for the smaller bush-like *Ambrosia deltoidea, Lycium andersonii*, or *Larrea tridentata* (Table 1). Given that a saguaro was growing in association with a tree-like perennial species (*C. microphyllum* or *O. tesota*), the probability that at least one other saguaro was growing within 2.5 m was 0.85; furthermore, the mean number of additional saguaros was 1.75. This contrasts markedly with the situation for saguaros growing in association with any of the three smaller perennial species, where the probability of at least one other saguaro being present within 2.5 m was 0.19, and the mean number of additional saguaros was 0.24. No saguaro found growing in the open had another saguaro growing within 2.5 m (Table 1).

TABLE 1—The mean number of additional saquaros within 2.5 m of subject saquaro under 6 different growing conditions at site 2.

Sole Associate Species	(N)	Mean ± s.d.	P(x)*
Olneya tesota	5	2.00 ± 1.00	1.00
Cercidium microphyllum	36	1.72 ± 1.34	.83
Ambrosia deltoidea	48	0.27 ± 0.57	.21
Lycium andersonii	5	0.20 ± 0.45	.20
Larrea tridentata	14	0.14 ± 0.36	.14
None (in open)	8	0.00 ± 0.00	.00

*P(x) = the probability of finding at least one additonal saguaro within a 2.5 m radius of subject saguaro (calculated as the proportion of (N) with at least one associated saguaro).

Two-meter tall saguaros are at that stage in their life history when thermal protection is no longer afforded by large nurse plants (Nobel, 1980). It is also when they first become reproductive (Steenbergh and Lowe, 1976, 1977). Consequently, that height was used to divide the saguaro data into two age classes (less than and greater than 2 m tall). The proportionate distribution of saguaros among associate categories did not change with age of saguaro at either of the two sites (Table 2). Each associate category was also considered separately to determine if more or fewer saguaros of a given age class occurred with a particular associate than expected from the proportion of all other saguaros in that age class. No significant changes in the degree of association with age of saguaro was found at either site (2 x 2 contingency tests, $P > 0.05$).

There was no relationship between height (age) of saguaro and height of associated *Larrea tridentata* ($X^2 = 2.1$, $P > 0.05$) or *L. andersonii* ($X^2 = 2.8$, $P > 0.05$). A significant positive association was found between saguaro height and height of both *Cercidium microphyllum* ($X^2 = 9.2$, $P < 0.05$) and *Posopsis juliflora* ($X^2 = 8.1$ $P < 0.05$), and a significant inverse relationship occurred between saguaro height and height of associated *Ambrosia deltoidea* ($X^2 = 18.2$, $P < 0.01$) (Table 3).

Saguaro seed density in the soil decreased uniformly and significantly (Friedman ANOVA, $P < 0.01$) from 5.33 ± 2.58 ($\bar{X}$ ± SD) seeds per tree (soil volume = 0.01 m) under the canopy of *Cercidium microphyllum*, to 1.17 ± 0.98 at the canopy edge to 0.17 ± 0.41 1 m from the canopy edge.

DISCUSSION—Saguaros were found growing in association with other plants significantly more often, and growing along significantly less often than expected on the basis of chance. A number of factors might contribute to the perpetuation of this nonrandom distributional pattern. Nurse plants could provide the only suitable micro-environment for successful seed germination (Steenbergh and Lowe, 1977). Nurse plants could provide a shaded environment, which would reduce the probability of seedling death due to heat stress or desiccation (Engelmann, 1859; Shreve, 1931b; Turner et al., 1966; Despain, 1974). Nurse plants might provide termal cover, which would prevent damage from frosts (Niering et al., 1963; Steenbergh and Lowe, 1976, 1977, 1983; Nobel, 1980). Nurse plants could also provide seedlings protection from predation and/or mechanical damage (Shreve, 1910; Niering et al., 1963; Niering and Whittaker, 1965; Turner et al., 1969; Steenbergh and Lowe, 1969, 1977).

TABLE 2.—The proportionate distribution of two age classes of living saquaro among various associate categories.

Site	Saguaro age class	A	B	C	D	E	F	G	Total
		Associate Category*							
Lower Bajada	Young (< 2 m)	44	24	0	8	14	19	5	114
	Old (< 2 m)	45	43	0	8	22	18	4	140
Rocky Basalt	Young (< 2 m)	14	40	2	36	0	12	10	114
	Old (< 2 m)	19	50	13	60	0	26	8	176

*A = *L. tridentata*, B = *A. deltoidea*, C = *L. andersonii*, D = *C. microphyllum*, E = *P. juliflora*, F = all other perennial species, G = open space. $X^2 = 4.70$, $P > .05$ and $X^2 = 8.45$, $P > .05$ for the lower bajada and rocky basalt sites, respectively.

There is an additional hypothesis, originally presented by Steenberg and Lowe (1977), that has received surprisingly little attention in the saguaro literature, but is worth further consideration. Nurse plants may contribute to the nonrandom distribution pattern of saguaros by providing extra protection for and/or dispersal sites for seeds. Although Steenbergh and Lowe (1977) document that high rates of seed predation exist, comparative rates from areas in the open versus areas beneath nurse plants have not been documented. Heteromyid rodents are major seed predators in desert systems (Brown et al., 1979; Reichman, 1979), but they are unlikely to produce the observed pattern because they forage most often beneath vegetation (Bowers, 1982). Ants or birds are also possible candidates, but the proportion of time that they forage in the open versus beneath vegetative cover is unknown.

It is also possible that seeds end up in relatively high densities beneath vegetation either because of physical forces (such as wind or water) or because of biological dispersal agents. For example, it is known that animals play a primary role in dispersal of seeds to sites suitable for germination and seedling establishment (Steenbergh and Lowe, 1977), but whether dispersal of seeds to these areas occurs disproportionately more often than to open areas is unknown. That biological dispersal agents may

TABLE 3—The relationships between saguaro height (age) and height class of 3 associated species (all associations significant; G-tests, $P < .05$).

Saguaro Height	Height class of *Ambrosia deltoidea* 0-.24m	.25-.49m	.50-.99m	Dead
<2m	5	12	42	5
>2m	12	40	41	0

	Height class of *Cercidium microphyllum* .5-.9m	1-1.9m	2-3.9m	4-8m	Dead
<2m	1	4	12	17	13
>2m	0	0	7	35	26

	Height class of *Prosopis juliflora* 1-1.9m	2-3.9m	4-8m	Dead
<2m	2	12	0	0
>2m	4	10	2	7

play at least a partial role in the development of the distribution pattern of saguaros is suggested from the finding that significantly more saguaros are found with the larger tree-like perennials than expected. The overabundance of saguaros under the large perennials may not be entirely due to the existence of better germinating or growing conditions there but, additionally, due to an expected bias in the dispersal of seeds. It is well known that birds disperse saguaro seeds (Steenbergh and Lowe 1969, 1977) and that they perch and roost disproportionately often in large trees (pers. obs.). This would lead toward the deposition of a disproportionately large number of seeds beneath the larger perennials. Precisely the same phenomenon can be used to explain the finding that saguaros grow in groups significantly more often under tree-like perennials than smaller perennials. Thus, both the occurrence of saguaros with larger trees more often than expected, and the frequent observation of relatively large numbers growing within 2.5 m of one another when beneath the canopy of tree-like perennials can be explained on the basis of a nonrandom seed dispersal pattern. An alternative explanation for the presence of groups of saguaros disproportionately often beneath large plants is that only large plants provide protective cover that extends over an area large enough to support the simultaneous growth of several saguaros.

The relative scarcity of saguaros in association with *Larrea tridentata* is puzzling. Either conditions for germination and growth are poor under *L. tridentata* (possibly because of the hydrophobic nature of the soils beneath that species; Adams et al., 1970), or a disproportionate number of seeds are removed from beneath *L. tridentata.* In either case, rodents may be more likely to eat seeds or damage seedlings beneath *L. tridentata* because that area is a common site for rodent burrows (Yeaton, 1978; pers. obs.) and for foraging activity of desert rodents (Bowers, 1982).

Why was there no change in composition of associates with saguaro age? The following three considerations are pertinent. Over 50% of the saguaros growing at each site were associated with the smaller nurse plants, regardless of saguaro age. There was a significant inverse relationship between saguaro age and height of a small shrub, *Ambrosia deltoidea* (Table 3). Small nurse plants such as *A. deltoidea, Menodora scoparia,* or *Emcelia farinosa* live less than 20 years (Shreve and Hinckley, 1937) as opposed to the 175-200 years of a saguaro. From these observations we conclude that, in the case of the smaller nurse plant species, the nurse plants may germinate and grow beneath older saguaros as often as the saguaros germinate and grow beneath older nurse plants. This, coupled with the long-term associations between saguaros and the larger perennial plant species, which live as long as saguaros themselves (Shreve and Hinckley, 1937), can explain the lack of change in composition of associate species through time.

This independence between the distribution of saguaros among associates and saguaro age also implies that any differential mortality among saguaros growing under different conditions (associate categories) has already taken place before the age of the youngest saguaros that we observed (about 10 cm, or 19 years old). This is consistent with the conclusions of Shreve

(1917), Turner et al. (1966), and Steenberg and Lowe (1977) that the protection a nurse tree gives is apparently most critical during the first few years of a saguaro's life, when they are only a few cm tall, or even still in the seed stage.

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