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SHADE AS A CAUSE OF THE ASSOCIATION BETWEEN THE CACTUS *NEOBUXBAUMIA TETETZO* AND THE NURSE PLANT *MIMOSA LUISANA* IN THE TEHUACÁN VALLEY, MEXICO

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SUMMARY

(1) The establishment phase of *Neobuxbaumia tetetzo*, a giant columnar cactus dominant in the Tehuacán Valley in central-southern Mexico, occurs mostly beneath the canopies of trees and shrubs which act as nurse plants. This pattern cannot be attributed to preferential seed dispersal, as *Neobuxbaumia* fruits open while still on the plant, dropping *c.* 1000 seeds fruit^{-1} randomly around the parent plant.

(2) An experimental field analysis of germination and survivorship of cohorts under different environmental conditions was performed in order to determine the underlying mechanisms associated to the establishment of *N. tetetzo* beneath the canopies of *Mimosa luisana*, a legume which is the most abundant shrub in the community. The experimental treatments followed a factorial design, with three levels of radiation (open space, artificial homogeneous shade and the shade produced by *Mimosa luisana*), two levels of predation (exclusion and non-exclusion of predators), and four topographic aspects (north, east, south and west).

(3) Seed germination was lowest in open spaces. In all treatments, exclusion from predators significantly increased seedling survival. Only the shaded treatments had live individuals at the end of the experiment, 2 years later. The results suggest that the nurse-plant effect between *Neobuxbaumia tetetzo* and *Mimosa luisana* is chiefly the result of differential survival in shaded microsites with less direct solar radiation, and consequently with lower daytime temperatures and lower evaporative demand.

(4) In order to determine the generality of these results, field samplings were conducted in two Mexican deserts located outside the tropical belt: the Vizcaíno Desert in Baja California and the Gran Desierto de Altar in Sonora. In these deserts direct solar radiation has a southern azimuth all year round. Five of six succulent species analysed showed a significant pattern of greater establishment on the shaded north sides of nurse plants.

(5) The amelioration of the physical environment produced by the nurse plants is important in the patch-structurated population dynamics of many communities of desert plants.

INTRODUCTION

In deserts the establishment phase of perennial plants occurs under unpredictable conditions of precipitation and in soils with high temperatures and low water content.

A knowledge of the dynamics of early seedling growth is important for an understanding of the dynamics of populations and the structure of desert communities. In many arid zones, the recruitment of several species occurs under perennial 'nurse' plants, which modify the environment beneath their canopies (e.g. Turner *et al.* 1966; McAuliffe 1988). Many explanations have been given for this phenomenon. The accumulation of seeds may be higher beneath perennial plants than in openings. Such non-random dispersion of seeds has been attributed to transport by animals (Olin, Alcorn & Alcorn 1989), wind (Went 1942) or water (Agnew & Haines 1960). Following germination, greater predation of individuals that are not hidden by the nurse plants (Niering, Whittaker & Lowe 1963; McAuliffe 1984b), the facilitation of seedling establishment by reduced direct solar radiation and lower soil temperatures beneath the nurse plant (Franco & Nobel 1989), the protection of seedlings during freezing periods (Steenbergh & Lowe 1977; Nobel 1980) and higher nutrient levels of the soil beneath canopies (García-Moya & McKell 1970) may enhance the survival of seedlings under perennial shrubs. Seed germination may be increased by the accumulation of fine wind-blown material that modifies soil structure beneath perennial plants (Wallace & Romney 1980).

In the Tehuacán Valley in central-southern Mexico, the giant columnar cactus *Neobuxbaumia tetetzo* (Weber) Backeberg, is a dominant species in an extensive vegetation type called 'Tetechera'. Most establishment of *N. tetetzo* occurs beneath the canopies of trees and shrubs (Valiente-Banuet, Vite & Zavala-Hurtado 1991). This association apparently contributes to a process of patch dynamics in which open spaces are initially colonized by shrubs. Later, these shrubs facilitate the establishment of cactus seedlings beneath their canopies. As the cacti grow, the nurse plants die and the older cacti are usually seen growing alone. The local exclusion of the most common shrub *Mimosa luisana* Brandeg by *N. tetetzo* is due to a competitive interaction (Valiente-Banuet, Vite & Zavala 1991). Yeaton (1978), McAuliffe (1984a) and Yeaton & Romero-Manzanares (1986) have reported similar recruitment and replacement processes in other shrub–cactus systems.

In this paper, an experimental analysis of the germination and survivorship of cohorts of *N. tetetzo* in the Tehuacán Valley under different conditions is described. Field observations in the temperate deserts of northern Mexico, designed to test the results derived from the Tehuacán experiment, are also described.

METHODS

Study site and species

The study was conducted in the semiarid Valley of Zapotitlán (18°20'N, 97°28'W), a local basin of the Tehuacán Valley in the state of Puebla, Mexico. This region owes its aridity to the rain shadow produced by the Eastern Sierra Madre (Smith 1965). It has an average rainfall of 380 mm, an annual mean temperature of 21 °C, and rarely freezes (García 1973). Soils are rocky, derived from sedimentary and metamorphic rocks. The main vegetation type is an arid tropical scrub ('matorral xerófilo', Rzedowski 1978) in which giant columnar cacti constitute dominant elements of the vegetation (Fig. 1). The study was made on a hill located inside the Botanical Garden of the Secretaría de Desarrollo Urbano y Ecología (SEDUE), located *c.* 30 km south of the city of Tehuacán. This is a mountainous zone in which *Neobuxbaumia tetetzo*,

FIG. 1. Arid tropical scrub in the Tehuacán Valley, Mexico. The shrubs are *Mimosa luisana* and the columnar cacti are *Neobuxbaumia tetetzo*.

a branched columnar cactus that may reach 12 m in height, is the dominant species, with densities of *c.* 1200 adults ha^{-1} (adults are arbitrarily defined as individuals >1 m tall). The flowering and fruiting seasons occur from mid-May until the end of June, just before the rainy season. First reproduction occurs when the plant is *c.* 2 m tall. The fruits open on the plant and although some of the seeds are removed by birds, most of the seeds (1−2 mm in diameter) fall to the ground forming a relatively uniform black carpet. Under laboratory conditions, 99% of seeds germinate.

Experimental design

Within the botanical garden, four 20-m × 20-m quadrats were located, each on a slope with a different aspect (north, east, south and west). The experimental treatments followed a factorial experimental design, with three levels of radiation (open space, artificial homogeneous shade, and the shade produced by *Mimosa luisana*), two levels of predation (exclusion and non-exclusion of predators, not distinguishing between vertebrates and invertebrates), and four different aspects (N, E, S and W). For each treatment, 180 seeds were sown in a 30-cm × 30-cm plot on 15 July 1988 (the seeds had been collected on June 1988 from ripe, open fruits; the fleshy mesocarp was dried and removed before planting). The soil surface was cleaned of other seeds before sowing seeds of *N. tetetzo* directly on the surface. Care was taken to minimize disturbance of soil structure. Rodents and birds were excluded by completely covering the experimental units with a 12-mm wire mesh with the bottom edges buried in the soil to a depth of 10 cm. Ants were excluded with an insecticide powder ('Clordane') which was applied every 3 days during the first week and every 8 days afterwards, until the seedlings were big enough to resist uprooting by ants. Shaded plots were established using green 1·5-mm nylon nets that were overlapped until photosynthetically active radiation (PAR) intensity was within one standard deviation

of the mean intensity beneath the canopies of *Mimosa luisana* at noon. PAR was
measured with a Licor quantum radiometer/photometer, model LI-185 A.

Nurse-shaded plots were always established in the base of *Mimosa luisana* individ-
uals of similar size, north of the main stem. Each of the twenty-four treatment com-
binations was replicated three times, giving a total of seventy-two experimental units.

Data analysis

Establishment of seedlings

Success in germination and initial establishment for the different treatments was
measured as the number of live seedlings present in each plot 1 week after sowing
(in moist soil, *N. tetetzo* germinates in *c.* 48 h). Differences were evaluated through
a contingency-table analysis made with a log-linear model (McCullagh & Nelder 1983).
The null hypothesis assumed an equal number of seedlings establishing in all the
treatments. Departures from this null model were examined for statistical significance.

Comparison of survivorship

Survivorship data among treatments were compared using log-linear models, con-
sidering time as a continuous variable and predation, aspect and shade as categoric
variables. The models were fitted with the Generalized Linear Interactive Modelling
statistical package (Baker & Nelder 1978) and the goodness-of-fit was evaluated with
a χ^2-test using the G statistic.

The model was based on the following assumptions. Consider a species with con-
stant mortality, d. In a cohort, by definition,

$$\frac{1}{N} \cdot \frac{dN}{dt} = -d. \tag{1}$$

Integrating eqn 1, $N_t = N_0 \exp(-dt)$, which can be also written as

$$N_t = \exp(a - dt), \tag{2}$$

where $a = \ln N_0$ and N_t is the number of survivors at time t. Equation 2 is a log-
linear model, which can be fitted through the corresponding statistical procedure
(McCullagh & Nelder 1983). This model describes a type II survivorship curve
(constant mortality rate; Pearl 1928).

If, on the other hand, mortality is not constant in time, eqn 1 can be written as

$$\frac{1}{N} \cdot \frac{dN}{dt} = -d + bt \tag{3}$$

Where d is the initial mortality rate at $t = 0$, and b is a parameter describing how this
initial rate is increased (if $b < 0$) or decreased (if $b > 0$) with time. Integrating eqn 3,
the analogue of eqn 2 for the case of varying mortality rates can be obtained:

$$N_t = \exp(a - dt + ct^2) \tag{4}$$

where d is the initial mortality rate, and the quadratic parameter $c = b/2$ is a measure
of the shape of the curve. All other symbols are the same as those in eqn 2. This
equation describes a log-linear model where the quadratic parameter c is a measure
of the intensity with which mortality rates vary in time. If $c < 0$, the initial mortality

tends to increase with time, and the model describes a type I survivorship curve. If $c > 0$, the initial mortality tends to decrease with time and the model describes a type III survivorship curve. If c does not differ significantly from zero, then the mortality rate tends to be constant in time and the best model is the one described in eqn 2. Thus, fitting eqn 4 to the data by means of a log-linear fitting procedure allows one to test hypotheses on the shape of the survivorship curve.

Field sampling in extratropical Mexican deserts

As an alternative test of the hypothesis that protection from radiation during the establishment phase is the main cause of the nurse-plant effect, the circular distribution of six succulent species around their nurse shrubs were measured in the Vizcaíno Desert in Baja California, Mexico (27°33′N, 113°12′W) and in the Gran Desierto de Altar in Sonora, Mexico (32°01′N, 113°31′W). Direct solar radiation has a southern azimuth all year round at these sites. (At Tehuacán, which is within the tropics, direct solar radiation near noon in summer comes from the north.) If the radiation hypothesis of the nurse-plant effect were true, a non-random circular distribution of saplings with respect to the nurse plant would be expected in the Vizcaíno and Gran Desierto sites, with preferential establishment towards the more-shaded north side of nurse shrubs.

The azimuthal frequencies of young individuals of six succulent species growing beneath perennial nurse shrubs were counted. Azimuthal categories were determined by dividing the circumference into four quadrants (north: 315° to 45°; east: 46° to 135°, and so on). Values of χ^2 were obtained by comparing the observed distribution with an expected uniform distribution. Five cactus species — *Carnegiea gigantea* (Engelman) Britton & Rose, *Ferocactus wislizenii* (Engelman) Britton & Rose, *Opuntia acanthocarpa* Engelman & Bigelow, an unidentified species of *Cylindropuntia* and *Pachycereus pringlei* (Watson) Britton & Rose) — and one euphorb — *Pedilanthus macrocarpus* Benth. — were chosen, without considering the identity of the nurse plants.

RESULTS

Germination and establishment

The first rains fell 2 days after the experiment began and germination occurred within 7 days. The number of live seedlings in each plot after the first week was higher under shaded treatments (Table 1). Although all factors and interactions were significant, radiation and predation explained 22% and 38% of the variation, respectively (60% pooled). The other terms (aspect and interactions) never explained more than 5% of the total variation and only explained 16·6% when pooled. In all cases, exclusion of predators significantly ($P < 0·005$) increased the number of established seedlings. The lower number of seedlings in the non-excluded treatments was associated mainly with the seed-removing activity of granivores. These granivores included birds (*Toxostoma curvirostre* Lafresnaye, *Columba livia* Gmelin, *Zenaida asiatica* L., *Z. macroura* L., *Columbina inca* Lesson and *C. passerina* L.), and harvester ants (*Pogonomyrmex* spp. and other unidentified species). Ants were also observed uprooting small seedlings.

TABLE 1. Total number of seeds of *Neobuxbaumia tetetzo* per treatment germinated and established after 7 days. Five hundred and forty seeds in each experimental condition were sown initially.

Predators	Open space	Artificial shade	*Mimosa* shade
North			
Excluded	31	163	125
Not-excluded	0	99	6
South			
Excluded	48	147	182
Not-excluded	3	71	9
East			
Excluded	48	138	138
Not-excluded	10	7	20
West			
Excluded	12	111	133
Not-excluded	7	5	5

The numbers of established seedlings in the non-excluded treatments did not differ between open spaces and beneath nurse plants ($P > 0.05$). Under artificial shade, however, predation was lower in south and north aspects than elsewhere. Without the effect of predators, exposure to direct solar radiation significantly decreased the establishment of seedlings. Furthermore, under conditions of predator exclusion no significant differences were found between the artificial shade and the nurse plant treatments.

Comparison of survivorship

The model fitted to the survivorship curves explained 89·1% of the variation. Time alone explained 47·6% of the total variation (survivorship frequencies are, by definition, a monotonically decreasing function of time), and time as a quadratic component explained 14·1% of the variation. Of the other statistical factors included in the model, the most important effect was the interaction between shade and time, which explained 11·1% of the variation. All other factors (radiation, predation and aspect, including all possible interaction terms) explained 16·3% of the variation, but no term explained individually more than 3%.

All the quadratic coefficients were positive and significantly different from zero, which indicates that all survivorship curves are type III, in which initial mortality is very high and tends to decrease with time (Fig. 2). In all cases, initial mortality rates were significantly higher in open spaces than in shaded conditions ($P < 0.005$; values in predator-excluded open spaces ranged between 0·12 and 0·26).

Additionally, these initial rates increased substantially in most of the non-excluded treatments, indicating that predation was very important once the seeds were on the soil (mortality rates in non-excluded open spaces varied between 0·25 and 1·00). The effect of predation, however, was not so marked in the artificial-shade plots.

At the end of the experiment, only the shaded treatments had live individuals, some of which survived 2 years after initiation (Fig. 2). The shaded treatments showed initial mortality rates and quadratic coefficients significantly lower than in open spaces ($P < 0.005$; initial mortality values ranged from 0·03 to 0·07). In the excluded and shaded treatments, survivorship curves were not significantly different between
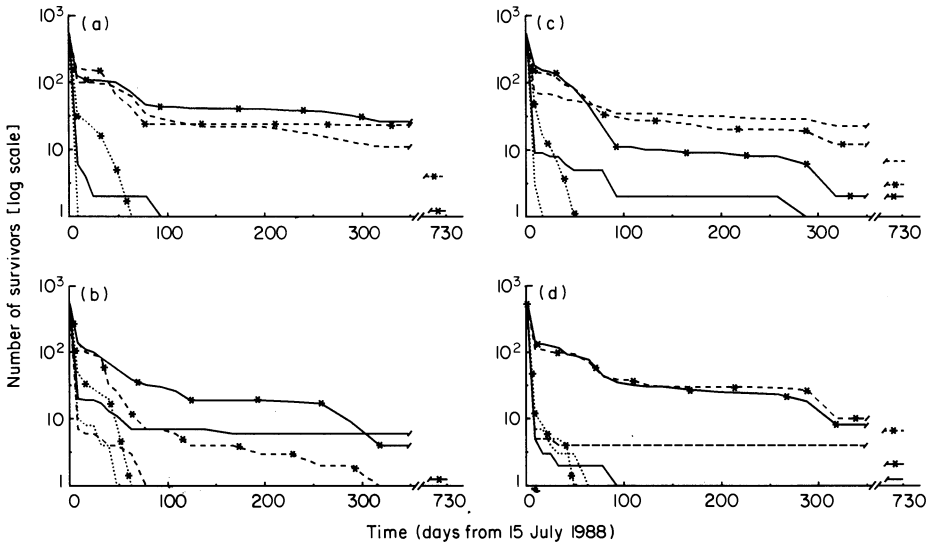
FIG. 2. Survivorship of cohorts of *Neobuxbaumia tetetzo* in (a) north, (b) east, (c) south and (d) west aspects of a hill, under different experimental treatments from July 1988 to July 1990. Lines with asterisks indicate predator-excluded treatments and without asterisks, non-excluded treatments: (———) beneath nurse plants; (_ _ _ _) under artificial shade; (.......) in open space.

the artificial and nurse-plant shades in any of the four aspects. The curves, however, were significantly different ($P < 0.05$) in the non-excluded conditions, and the pattern varied according to the aspect of the plot. In the north, south and west aspects survivorship was higher under artificial shade, but in the east aspect it was higher under the nurse plants. This pattern may have arisen from the patchy foraging behaviour of the predators already mentioned. Although substantial mortality was registered during the second year, it seems to be largely independent of the exclusion of herbivores (the low number of individuals remaining at the end of the second year did not allow a *G* test).

Distribution of saplings in extratropical deserts

In the Vizcaíno and Altar deserts, all the species with the exception of *Ferocactus wislizenii*, showed a significantly non-random distribution with preferential establishment towards the north of their nurse shrub (Fig. 3).

DISCUSSION

Several studies have analysed the establishment of succulents under field conditions. For example, a large proportion of the seed crop of the giant columnar cactus *Carnegiea gigantea* is consumed by birds while the fruits are on the plant and another large proportion is removed by birds, mammals and insects (mainly harvester ants) when the seeds are on the ground (Steenbergh & Lowe 1969, 1977). Consequently a very small percentage of seeds ($<10^{-3}$) remains on the ground until suitable conditions for germination occur during the summer. According to our observations on
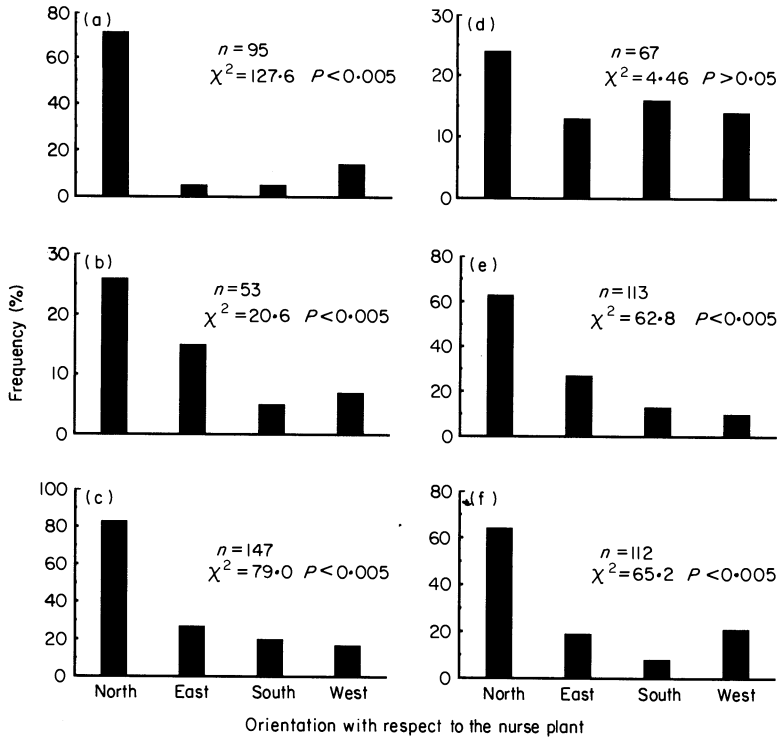
FIG. 3. Circular distribution of saplings of six succulent species with respect to perennial shrubs in the Gran Desierto de Altar and in the Vizcaíno Desert, Mexico: (a) *Carnegiea gigantea*, (b) *Opuntia acanthocarpa*, (c) *Pachycereus pringlei*, (d) *Ferocactus wislizenii*, (e) unidentified *Cylindropuntia* sp. and (f) *Pedilanthus macrocarpus*.

Neobuxbaumia tetetzo, the most important effect of the seed removers seems to occur once the seeds are on the ground, probably because the fruits of *N. tetetzo* have a colourless fleshy pulp which contrasts with the bright red fleshy pulp of *Carnegiea gigantea*, which serves as a visual attractant for frugivorous birds. The thousands of seeds of *N. tetetzo* that fall uniformly to the ground are removed intensively by ground-foraging birds and also by harvester ants. This harvester activity occurs similarly in open spaces and under nurse plants, indicating that differential mortality of seeds by preferential predation in some patches is not occurring in the study site. The lower predation rates found in some artificially shaded treatments when compared with those beneath nurse-plant plots, are probably due to the alteration of predator behaviour by the plastic mesh. The demographic fate of the seeds removed by the different granivores is unknown; our observations indicate that most of the seeds removed by ants die, but the fate of those consumed by birds is still unknown. In the case of *Carnegiea gigantea*, birds may disperse the seeds under the canopies of shrubs and trees, thus further contributing to the nurse-plant effect (Steenbergh & Lowe 1977; Hutto, McAuliffe & Hogan 1986; Olin, Alcorn & Alcorn 1989).

The importance of soil moisture for the germination of seeds under field conditions has been associated with variation in microrelief and with the presence of protected microsites (Harper, Williams & Sagar 1965). The lowest number of seeds that germinated in this study occurred in openings in which solar radiation heats the surface.

This heating may reduce soil moisture to levels beneath that required for germination. This hypothesis is further supported by the observation that in openings most of the seeds germinated when they were next to or beneath stones. Very few seeds managed to germinate in completely open spaces. Larmuth & Harvey (1978) found that the presence of stones is of vital importance for germination and survival of seedlings in south-eastern Morocco, because of their role as dew collectors. In the Tehuacán Valley, stones clearly help to maintain humidity for a short time, but their role in long-term survival does not seem to be of major importance.

The best conditions for germination were in shaded sites where evaporative demand is lower and, consequently, where soil moisture is more adequate. According to Steenbergh & Lowe (1977), moisture availability is sufficiently prolonged in shaded sites to permit germination. Additionally, lower transpiration of desert plants and lower water output have been reported for shaded conditions in wadis by Abd El Rahman & Batanouny (1965a,b) when compared with open spaces. In comparing the microclimate beneath shrubs and in open spaces, Shreve (1931) also concluded that vegetational differences between these patches were associated with differences in solar radiation, which modify soil temperatures and rates of transpiration. In the Zapotitlán Valley, soil temperatures beneath and between perennial plants reached a maximum difference of 16 °C in the summer (Valiente-Banuet et al. 1991).

Microclimatic differences between open and shaded conditions were reflected in the survivorship observed. Only the shaded treatments had live individuals 2 years after initiation of the experiment. All the unshaded seedlings were dead in <100 days, a result also reported for both Carnegiea gigantea (Turner et al. 1966) and Agave deserti (Jordan & Nobel 1979). In both of these studies, seedlings died even with watering, a result that shows the lethal effect of high temperature for succulent plants with the CAM photosynthetic pathway.

In shaded, predator-excluded treatments, no differences between the artificial shade and the nurse–plant effect were found. As the artificial shade plots were located on sites that were previously open spaces, these similar survivorship patterns suggest that the differences in soil properties reported for both kind of patches (Valiente-Banuet, Vite & Zavala-Hurtado 1991) were not important for seedling survival. However, higher nutrient levels encountered beneath nurse plants have been shown to modify the rates of growth of cacti (Turner et al. 1966; Franco & Nobel 1989), and also of certain non-succulent plants (Halvorson & Patten 1975). The relationship between nurse-plants and nutrient levels, and its effect on the survivorship and growth of cacti, should be analysed in more detail because faster growth rates may increase the probability of seedling survival, by allowing a more rapid escape from the critical stages of early growth. Jordan & Nobel (1981) have reported that the volume of water stored is critical for determining the length of time succulents can survive during extended droughts.

The germination and survivorship results reported here indicate that radiation and its associated factors, temperature and evaporation, determine the interspecific association between Mimosa luisana and Neobuxbaumia tetetzo. The same observation also has been made by Turner et al. (1966) and Franco & Nobel (1989) for the columnar cactus Carnegiea gigantea, and by Halvorson & Patten (1975) for non-succulent plants. In short, our experimental results suggest that excessive radiation, evaporation and temperature in open spaces, and the resulting mortality, are the main cause of the nurse-plant effect.

The azimuthal frequency distributions of five of the six species of saplings studied in the Vizcaíno and Altar deserts support the hypothesis that the amelioration of the physical environment, in terms of radiation, evaporative demand and temperature, are the main factors related to location of CAM succulents beneath nurse plants. These observations also indicate that besides the different qualities of nurse plants, it is possible that slight gradients at a very small scale are operating beneath the canopies within each patch. This has also been suggested by Shmida & Whittaker (1981) for annuals growing in association with perennial plants. Franco & Nobel (1989) found that *Carnegiea gigantea* seedlings were more associated with the base than with the edges of the nurse plants. Shade as the main explanation of nurse-plant associations does not exclude the possibility of other factors such as seed dispersal reinforcing this effect. In the case of *Ferocactus wislizenii*, which showed a random circular distribution with respect to the nurse plants, the individuals avoid direct solar radiation and excessive heat load by growing with an inclination towards the south; this growth pattern has also been reported for several species of *Copiapoa*, a Chilean barrel cactus (Ehleringer *et al.* 1980). This capacity to regulate direct radiation possibly explains its lack of a significant azimuth with respect to the nurse plant.

In conclusion, the nurse-plant effect in arid and semi-arid regions is chiefly the result of differential survival in shaded microsites with less direct solar radiation, and consequently, with lower daytime temperatures and lower evaporative demand. Differences in soil fertility under nurse plants are of secondary importance, at least in our study area. We can conclude that the limitations imposed by radiation on the spatial distribution of seedling establishment and survival are of primary importance as driving forces in the patch-structured dynamics of many desert plant communities.

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