SPATIAL DISTRIBUTION OF THREE GLOBOSE CACTI IN RELATION TO DIFFERENT NURSE-PLANT CANOPIES AND BARE AREAS

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ABSTRACT—We report the frequency of 3 globose cacti (*Mammillaria carnea, M. haageana,* and *Coryphantha pallida*) associated with nurse plants or bare areas and assess the size of plants in each site. We found 3 times more cacti established beneath nurse plants than in bare areas, and all cacti species were the same size when associated with shrub cover or bare areas. Under a plant canopy, the size structure was pyramidal, whereas in bare areas, individuals were found isolated with an even size structure, and few small plants were recorded. There was a positive relationship between the type of shrub cover and the associated globose cacti. We found more individuals of all 3 species of cacti associated with *Prosopis laevigata* than with *Mimosa luisana,* but size structure was similar between them. We discuss 2 possible scenarios that may result from the nurse-protégé interaction.

RESUMEN—Registramos la frecuencia de establecimiento do tres cactáceas globossas (*Mammillaria carnea, M. haageana* y *Coryphantha pallida*) asociadas con plantas nodriza y en áreas rasas y evaluamos el tamaño de las plantas en cada sitio. Encontramos 3 veces más cactáceas establecidas debajo de plantas nodriza que en áreas rasas, y todas las especies de cactáceas fueron del mismo tamaño cuando se asociaron con áreas cubiertas de arbustos o con áreas rasas. Bajo la cubierta de las plantas, el tamaño estructural fue piramidal, mientras que en áreas rasas, se encontraron individuos aislados con un tamaño estructural parejo y se registration pocas y pequeñas plantas. Hobo una relación positivia entre el tip de cubierta de arbusto y la cactácea globosa asociada. Encontramos más individuos de las tres especies de cactaáceas asociadas con *Prosopis laevigata* que con *Mimosa luisana,* pero el tamaño estructural fue similar entre ellas. Discutimos 2 posibles escenarios que pueden resultar de la interacción entre nodriza y protegido.

Establishment of Cactaceae beneath the canopy of nurse plants has been described for a variety of life forms (i.e., columnar, globose, cylindropuntias, platiopuntias; Steenbergh and Lowe, 1969; Turner et al., 1969; McAuliffe, 1984*a*; Franco and Nobel, 1989; Valiente-Banuet and Ezcurra, 1991; Cody, 1993; Suzán et al., 1994; Mandujano et al., 1998; Rodríguez and Ezcurra, 2000). However, not all individuals of a given species are associated with nurse plants because plants also can be found in bare areas without the apparent protection provided by the canopy of a nurse plant. This suggests that not all species of Cactaceae require nurse plants (Nobel et al., 1986; Rodríguez and Ezcurra, 2000) or that individuals may tolerate unprotected environmental conditions (e.g., Nobel, 1984; Mandujano et al., 1998). Ecological explanations of nurse plant interactions have been proposed. For example, the pattern of establishment under nurse plants could result from nonrandom dispersal of seeds (Steenbergh and Lowe, 1969), or be explained by environmental requirements of seedlings that need the protection of a nurse to avoid high solar radiation, excessive water loss, freezing, and predation (Nobel, 1980; Vandermeer, 1980; McAuliffe, 1984*a*; Valiente-Banuet and Ezcurra, 1991; Cody, 1993; Mandujano et al., 1998).

The nurse protégé relationship is not always beneficial, as environmental requirements of plants change throughout their life cycle. Some authors have shown that the presence of a protégé alters growth and survival of the nurse plant (Yeaton, 1978; McAuliffe, 1984*b*; Flores-Martínez et al., 1994). Others have shown that the benefits provided by the nurse plant may eventually introduce competitive interactions for water and light that can have a negative effect on protégé growth rates (Franco and Nobel, 1988, 1989; Briones et al., 1996; Mandujano et al., 1998). In addition, seedling survival also will be determined by other ecological conditions related to the quality of the protection provided by the nurse-plant (e.g., plant architecture, buffering capacity against environmental conditions, photosynthetically active radiation (PAR) interception) as these can have an important effect on seedling growth and survival (Patten, 1978; Smith et al., 1987; Mandujano et al., 1998; Mandujano et al., 2001). The wide range of conditions that are involved in the nurse-protégé relationship must be evaluated for protégés in different stages of their life cycle, and beneath the canopy of different nurse plants. It is therefore important to determine quality of protection provided by different species and to determine the species that require a nurse plant.

In the Tehuacan-Cuicatlan Valley (Mexico), the globose cacti *Mammillaria carnea* Zucc. Ex Pfeiff., *Mammillaria haageana* Pfeiff. (=*Mammillaria collina* (Purp.) Britton and Rose), and *Coryphantha pallida* Britton and Rose (Bravo-Hollis, 1978), can be found under the canopy of perennial shrubs and in bare areas. In this study, we determined the number of individuals of globose cacti that established under the canopy of *Mimosa luisana* Brand and *Prosopis laevigata* (Humb. and Bonpl. ex Willd.) M.C. Johnst. (Leguminosae) as well as in areas with no canopy protection. To determine the success of these 3 globose cacti, we used cacti size as the measure of overall plant performance. Given that desert environments pose harsh environmental conditions, most of the plants found would be expected to be established beneath the canopy of nurse plants. The ecological hypothesis was that under *M. luisana* (deciduous plants that shed leaves in November and produce new foliage in February) globose cacti will establish less frequently and will be smaller than cacti that establish under a prolonged shade such as that provided by *P. laevigata* (deciduous plants that gradually replace leaves from December to February). We evaluated the distribution of globose cacti and the quality of nurse plants. The specific questions addressed were: 1) what is the distribution of globose cacti between nurse plants and bare areas, and 2) are there size differences between the globose cacti beneath nurse plants or bare areas?

MATERIALS AND METHODS—Field work was conducted at the Helia Bravo Botanical Garden in the Tehuacan-Cuicatlan Valley, Tehuacan, Puebla, Mexico (17°48′ and 18°58′N, 97°03′ and 97°43′W; Jaramillo and González-Medrano, 1983). Vegetation of the area is dominated by the columnar cactus *Neobuxbaumia tetetzo,* and associated woody perennials are *Acacia constricta, Cercidium praecox, Castela texana, Mimosa luisana,* and *Prosopis laevigata* (Rzedowski, 1978; Zavala, 1982; Montaña and Valiente-Banuet, 1998). The dominant perennials at the study site are *M. luisana* and *P. laevigata.* Mean annual precipitation is 380 mm concentrated during the summer season with a mean annual temperature of 21.2°C (García, 1973; Valiente-Banuet, 1991; Montaña and Valiente-Banuet, 1998).

In 1993, we randomly established 9 50 by 4 m plots in a north to south orientation to locate nurse plants. Orientation was fixed to avoid a sampling bias as some species commonly establish in an east to west position but other species do not show orientation preferences (Rodríguez, 1998; Rodríguez and Ezcurra, 2000). Under each potential nurse plant, we established a 50-cm wide transect that covered the radius of the canopy and an area of similar size in a bare area beside the nurse plant. Because each radius varied in length, and to compare among canopies, the radii of the canopies were divided into 5 standard segments (0 to 20, 20.01 to 40, 40.01 to 60, 60.01 to 80, 80.01 to 100%) that corresponded to the proportional distance from the shrub's base to the edge of the canopy. In each transect we determined the number, species, location, and diameter (cm) of globose cacti. The number of individuals under nurse plants and in bare areas were pooled by species. Comparisons were carried out using Chi-square tests followed by residual analysis in order to determine: 1) whether the frequency of globose cacti was statistically different between locations (under a shrub's canopy or on bare areas) with respect to the frequencies of globose cacti expected under the relative cover of nurse plants or bare areas (using a 3 by 2 contingency table); 2) if there were differences in the frequency of cacti between shrub species along the segments of the transect (2 by 5 contingency table); 3) if the frequency of each cactus species differed between nurse plants and bare areas (2 by 2 contingency table); and 4) if there were differences in the distribution of cacti along the segments of the transect between nurse plants (5 by 3 contingency table; Zar, 1974; Crawley, 1993).

Individuals of the 3 species of globose cacti were classified into 4 diameter classes. The maximum size (diameter) of those globose cacti growing beneath either *M. luisana* or *P. laevigata* was compared with that of those cacti growing on bare areas by means of Student's *t* tests. We contrasted the maximum size value among protégé sizes to explore the existence of a better microsite condition under different nurse plants. We did not use the average to compare sizes because beneath the canopies there was a pyramidal size structure, whereas in bare areas there were few individuals. The size distributions of globose cacti growing either under the shrubs or on bare areas were compared to the frequencies expected from the null hypothesis of equal distribution, by means of a Chi-square test and residual analyses (4 by 3 contingency table; Zar, 1974; Everitt, 1977).

RESULTS—We found that 86% of the shrubs had globose cacti associated with their canopy ($n = 57$, *M. luisana*; $n = 40$, *P. laevigata*). Comparing the observed frequencies of globose cacti established in bare areas or beneath perennial nurse plants with the frequencies of globose cacti expected under the relative cover of nurse plants or bare areas in the sampled plots, there were more cacti associated with nurse plants ($\chi^2 = 405$, $P < 0.001$, $df = 2$; Fig. 1). In a detailed comparison between each shrub species we found 1.4 times more globose cacti associated with *P. laevigata* than with *M. luisana* (206 and 147, respectively; $\chi^2 = 18$, $P < 0.02$, $df = 4$); there was a weak relationship between nurse plant size and the number of associated globose cacti ($r^2 = 0.17$, $P = 0.01$), suggesting that factors other than nurse plant size are responsible of the abundance of protégés beneath them.

A comparison among the 3 globose cacti species showed that they were commonly established beneath the canopy of both shrubs. *Mammillaria carnea* was 9.5 times more common under shrubs than in bare areas ($\chi^2 = 178.5$, $P < 0.05$, $df = 1$; Fig. 1A), *M. haageana* was 3 times more frequent under nurse plants than without them ($\chi^2 = 24.5$, $P < 0.05$, $df = 1$; Fig. 1B), and *Coryphantha pallida* was 4 times more common under nurse plants ($\chi^2 = 38.6$, $P < 0.05$, $df = 1$; Fig. 1C). The highest frequencies of individuals from *M. carnea* and *M. haageana* were closest to the center of the shrub canopies (0 to 20 and 20 to 40% of the canopy distance; 75% and 49%, respectively, $\chi^2 = 58.2$, $P < 0.05$, $df = 8$; Fig. 1A, B). Residual analyses suggested that both species of *Mammillaria* were established more frequently in the 2 areas closest to the canopy center, whereas *C. pallida* did not differ between canopy categories (Fig. 1C).

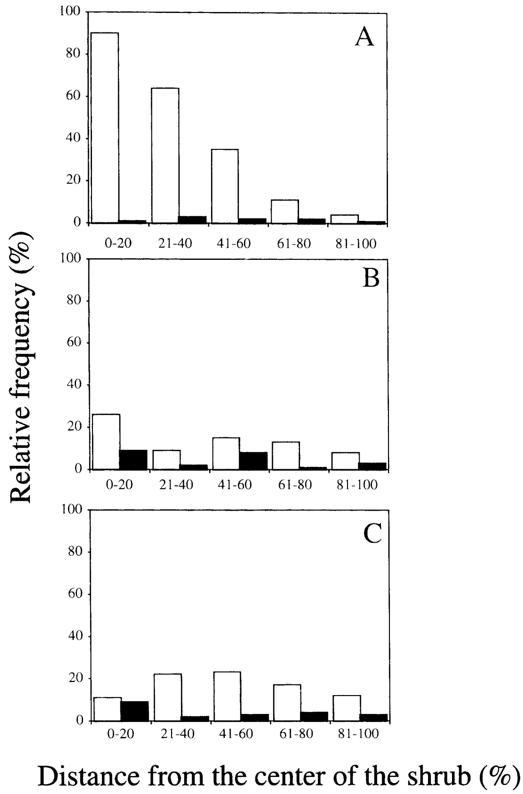

FIG. 1—Frequency distributions of A) *Mammillaria carnea,* B) *Mammillaria haageana,* and C) *Coryphantha pallida* along the canopy of the nurse plant and in bare areas. Distance is presented as a percentage to standardize the effect of canopy size. Beneath nurse plants (open bars), bare areas (solid bars).

The maximum and average size (diameter) of globose cacti did not differ between plants established beneath *M. luisana* or *P. laevigata* and plants in bare areas ($P > 0.5$; Table 1, Fig. 2). Under the hypothesis of equal distribution of globose cacti of all size-classes between those associated to nurse plants and in bare areas, we found more plants associated with nurse

TABLE 1—Mean (± 1 *SE*) and maximum size (diameter cm) of globose cacti established beneath the canopy of nurse plants (*Mimosa luisana* or *Prosopis laevigata*) and in sites without plant cover (bare areas).

	Nurse					
	Mimosa luisana		*Prosopis laevigata*		Bare area	
Cactaceae	Mean	Max	Mean	Max	Mean	Max
Mammillaria carnea	5.8	19	5.5	34	6.6	22
n = 231	(0.47)		(0.37)		(1.09)	
Mammillaria haageana	7.6	28	9.8	32	5.8	25
n = 97	(0.99)		(1.67)		(1.05)	
Coryphantha pallida	4.4	21	5.9	17	4.9	16
n = 109	(0.51)		(0.62)		(0.72)	

plants than in bare areas ($P < 0.0001$; Fig. 2). For all size classes, globose cacti were more frequently associated with *M. luisana* ($P < 0.001$) or *P. laevigata* ($P < 0.001$) in comparison to areas without plant cover (Fig. 2), but the number of cacti among size classes did not differ between nurse plants ($P > 0.48$).

DISCUSSION—More individuals of *Mammillaria haageana, M. carnea,* and *C. pallida* were associated with *M. luisana* and *P. laevigata* than with bare areas. In general, the majority of globose cacti followed a log normal distribution beneath the canopy, with a high frequency in the first and second categories (0 to 40%) that decreased towards the edge of the canopy. The nurse plant that had the highest number of associated cacti was *P. laevigata*. The ability of *P. laevigata* to retain its leaves for a long time may facilitate cacti survival and establishment. Other authors have found that *Prosopis* species support several cacti and other plant species associated with their cover (Valiente-Banuet et al., 1991; Suzán et al., 1994; Fulbright et al., 1995; Mandujano et al., 1998). It seems that Cactaceae species frequently associate with nurse plants that provide a more constant and durable canopy such as *Prosopis*. This suggests that cacti species indeed benefit from the protection from excessive solar radiation and the lower temperatures provided by nurse plants beneath the canopy (18 to 25°C under the canopy and 18 to 40°C in bare areas during a 24 h period; Valiente-Banuet et al., 1991). Similar to our results, it has been reported that protégés (subject to the same water availability) accumulated more biomass under shaded conditions than growing in bare areas (Nolasco et al., 1997; Mandujano et al., 1998). Possibly, as cacti are less subject to a thermal stress beneath nurse plants, resources may be invested in other functions such as growth.

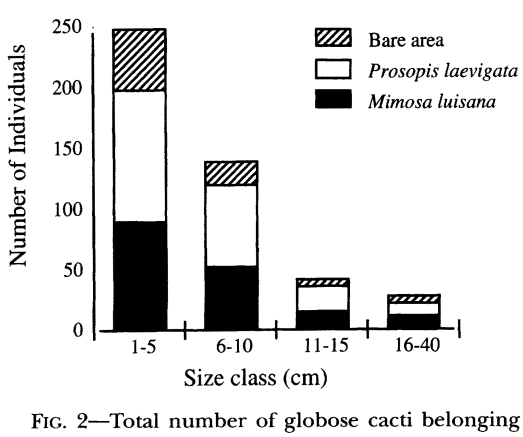

FIG. 2—Total number of globose cacti belonging to 4 different size classes established beneath the canopy of shrubs or in bare areas.

The differences we found in the size distribution between the established individuals protected beneath the canopy of nurse plants and in bare areas can have 2 possible causes. First, individuals establish more frequently under the canopy of nurse plants, and the over representation of individuals in the 1 to 5 cm category is the accumulated success of establishment over several years. However, measuring seedling establishment in any given point in time (without a history of the system) overestimates the recruitment rates of seedlings as these can remain the same size for more than a 5-year period. Furthermore, even in safe sites provided by nurse plants, recruitment rates can vary between years (Mandujano et al., 2001). The second possibility is that protected seedlings have different mortality or growth rates depending on whether they are associated with nurse plants as well as which specific species they associate with (e.g., Steenbergh and Lowe, 1969; Yeaton, 1978; Valiente-Banuet and Ezcurra, 1991; Suzán et al., 1994; Mandujano et al., 1998). For example, if seedlings in bare areas have higher mortality, we would rarely find representatives of small sizes (seedlings and juveniles) such as the low frequency found in this study. Other authors have found that under natural conditions, seedlings established in bare areas are rapidly removed by herbivores (Steenbergh and Lowe, 1969; Turner et al., 1969; McAuliffe, 1984*a*; Cody, 1993; Mandujano et al., 1998). In contrast, Mandujano et al. (2001) have reported that seedlings of *Opuntia rastrera* established experimentally (in the same year) beneath a deciduous shrub (*Jatropha dioica*) that extinguishes close to 40% of photosynthetically active radiation grew faster than seedlings that are associated to another nurse plant (*Hilaria mutica*) that extinguishes 90% of PAR, even though survival is higher under the grass (*H. mutica*). Unfortunately in this study, we are unable to discriminate between these 2 possibilities. We would require long-term demographic and ecological studies to determine the influence of seedling recruitment and the effects of herbivory over long time periods.

In relation to establishment of cacti in bare areas Nobel et al. (1986) found that globose cacti did not have mechanisms to control temperature; they increase or decrease their temperature according to soil temperatures without evidence of tissue damage. Apparently, the production of heat-shock proteins prevents tissue degradation even at high temperatures (Chuan Kee and Nobel, 1986). However, harsh environmental conditions in bare areas resulted in low recruitment, as very few cacti can establish in these microsites and the plants that can establish are smaller than those associated with shrubs. Furthermore, spine patterns influence establishment by providing protection against excessive solar radiation. Rodríguez (1998) found that species that are heavily covered with spines such as *Mammillaria pectinifera* can be found under nurse plants and in bare areas, and those having reduced spine cover such as *M. carnea* were mostly found under nurse plants, suggesting that spines are effective protection against solar radiation. Our results suggest that under *M. luisana* and *P. laevigata* there are significantly more established individuals than in bare areas, which supports the hypothesis that *M. carnea* requires nurse plants to establish.

There are other factors that were not evaluated in this study that can contribute to the establishment of globose cacti in bare areas. The protection projected by the canopy of nurse plants can be extended to bare areas at certain times of day, indirectly acting as nurse plants. Thus, if the distance between neighboring nurse plants is sufficiently small, plants in bare areas are in fact influenced by the canopies of the surrounding nurse plants, even though they may not be strictly beneath the canopy of a shrub. Possibly, all the individuals in bare areas associate with annual plants that function as ephemeral nurse plants, during sporadic temporal windows or establish in bare areas but under extremely favorable conditions (i.e., high precipitation).

In general, the nurse-protégé relationship shows a cost-benefit balance to the protégé, and this can be of 2 kinds in relation to the nurse quality. The interaction begins with benefits to the protégé in the first steps of its development, when seedlings have C_3 photosynthesis (Altesor et al., 1992) and they require the protection from harsh abiotic conditions. However, in later life cycle stages, the protégé should pay the benefit of establishment decreasing in growth rate because of competition for light or water with the nurse plant. In particular, this has been suggested for grassy nurse plants (Franco and Nobel, 1988, 1989; Mandujano et al., 1998). Alternatively, the interaction is beneficial throughout the different life cycle stages of the protégé. Some deciduous shrubs (e.g., those reported in this study) facilitate the establishment and confer protection from abiotic factors in specific times of the year. Our data support the benefits of open deciduous canopies for establishment and growth of globose cacti.

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