ECOTRÓPICOS 21(2):97-105 2008
Sociedad Venezolana de Ecología

SPATIAL ASSOCIATIONS BETWEEN TWO GLOBOSE CACTI AND TWO DOMINANT MIMOSOID BUSHES IN A TROPICAL SEMIARID ENCLAVE

RELACIONES ESPACIALES ENTRE DOS CACTÁCEAS GLOBULARES Y DOS ARBUSTOS MIMOSOIDES EN UN ENCLAVE SEMIÁRIDO TROPICAL

Daniel M. Larrea-Alcázar[1,2], Johnny J. Murillo[3], Carmen J. Figueredo[3,4] & Pascual J. Soriano[1,3]

[1]Postgrado en Ecología Tropical (PET), Instituto de Ciencias Ambientales y Ecológicas (ICAE), Universidad de Los Andes (ULA), Mérida 5101, La Hechicera, Mérida, Venezuela.

[2]Current address: Centro de Análisis Espacial (CAE), Instituto de Ecología (IE), Universidad Mayor de San Andrés (UMSA), A.P. 10077 Correo Central, Phone: 591-2-2791141, Fax. 591-2-2797511, E-mail: larrea.alcazar@gmail.com, La Paz, Bolivia.

[3]Departamento de Biología, Facultad de Ciencias, Universidad de Los Andes (ULA), Mérida, Venezuela.

[4]Laboratorio de Biología de Organismos, Centro de Ecología, Instituto Venezolano de Investigaciones Científicas (IVIC), Caracas, Venezuela.

ABSTRACT

Spatial relationships between two globose cacti (*Mammillaria mammillaris* (L) Karsten and *Melocactus schatzlii* Till & Gruber) and two dominant mimosoid shrubs (*Acacia farnesiana* (Willd.) L. and *Prosopis julifora* DC.) were evaluated in two habitats (cactus thicket and thornscrub) of a Venezuelan semi-desert mountain valley. Globose cacti and shrubs are spatially associated, mainly in the cactus thicket, suggesting that cacti probably benefit from shrubs for their recruitment (*sensu* nurse plant syndrome). The presence of cacti in open areas, however, suggests that the need of a nurse plant for establishment of both globose cacti may be highly facultative. This is the first assessment reporting a positive globose cactus-shrub spatial association from the Andes of northern South America. By confirming that mimosoid shrubs can influence the spatial distributions of globose cacti, this observational approach provides a foundation for future research and essential information to increase our knowledge on the role of mimosoid bushes as nurse plants in the tropical Andes.

Palabras clave: Andes, facilitation, globose cacti, *Mammillaria, Melocactus*, semi-arid zones, spatial arrangement

RESUMEN

Evaluamos la relación espacial entre dos cactáceas globulares (*Mammillaria mammillaris* (L) Karsten and *Melocactus schatzlii* Till & Gruber) y dos arbustos mimosoideos (*Acacia farnesiana* (Willd.) L. and *Prosopis julifora* DC.) en dos hábitats (“cardonal” versus “espinar”) de un enclave semiárido de Los Andes venezolanos. Nuestros resultados muestran que ambas especies de cactáceas globulares crecen espacialmente asociadas a ambas especies de arbustos mimosoideos (principalmente en al cardonal estudiado). Estos resultados sugieren que la regeneración natural de ambas cactáceas probablemente es favorecida por la proximidad de estos arbustos (*sensu* síndrome “planta nodriza”). No obstante, la presencia de ambos cactus en espacios abiertos apunta a que la necesidad de una planta nodriza para su reclutamiento puede ser altamente facultativa. Este es el primer estudio que reporta asociaciones espaciales positivas entre cactáceas globulares y arbustos mimosoideos en los Andes del norte de Sudamérica. Al confirmar que ambos arbustos mimosoideos pueden influir la disposición espacial de cactáceas de forma globular, proporcionamos las bases para futuras investigaciones y presentamos información clave sobre el rol que juegan estos arbustos como plantas nodriza en Los Andes tropicales.

Key words: Andes, cactáceas globulares, disposición espacial, facilitación, *Melocactus, Mammillaria*, zonas semiáridas

INTRODUCTION

Cacti are a very diverse plant family comprising more than 2000 species, most of which are native and endemic to arid and semi-arid environments of the Neotropical region (Godínez-Álvarez *et al*. 2003). Many species of cacti grow spatially associated with mimosoid shrubs, which can modify soil properties and microclimate conditions below their crowns compared to surrounding open areas, and favour cactus germination and establishment (Valiente-Banuet and Ezcurra 1991, Valiente-Banuet *et al.* 1991, de Viana *et al.* 2001, Tewksbury and Lloyd 2001, Flores and Jurado 2003, Suzán-Azpiri and Sosa 2006, López and Valdivia 2007, Larrea-Alcázar and Soriano 2008). Although cacti-shrub associations have been well documented, our knowledge about the importance of the so-called nurse-plant syndrome phenomenon for the spatial distribution of globose cacti is still scarce (Suzán *et al.* 1996, Mandujano *et al*. 2002, Reyes-Olivas *et al*. 2002). Facilitation seems to be less important for this growth form of cactus because, while preferring microhabitats underneath shrubs, they may be capable of establishing in open ground suggesting that positive globose cacti-shrub associations are facultative (Mandujano et al. 2002, Godínez-Álvarez et al. 2003, López and Valdivia 2007).

Along the Andes of northern South America, several dry valleys occur which are geographically isolated, have similar physiognomy and constitute an archipelago of small semi-arid patches from Cordillera de Mérida (western Venezuela) through Colombia to Ecuador (Sarmiento 1972, Soriano and Ruíz 2002). The Lagunillas enclave, the biggest of this type in the Venezuelan Andes, contains mimosoid shrubs and columnar cactus species as the prevailing elements of its xerophyllous vegetation, which can form a habitat mosaic from cactus thicket to thornscrub sites. As in other semi-arid tropical zones, the effect of these mimosoid shrubs on the spatial distribution of columnar cacti has been demonstrated (Larrea-Alcázar and Soriano 2008). However, there is no information indicating if other associations with mimosoid legumes are occurring at the enclave involving different growth forms of cacti. This information should help us to determine the overall importance of mimosoid species as nurse plants for the natural regeneration of different cactus species in the tropical Andes.

One commonly used approach to test for a positive cactus-shrub relationship is to conduct field experiments in which cactus seedlings are planted both below a shrub's canopy and in open areas (Valiente-Banuet and Ezcurra 1991, Suzán-Azpiri and Sosa 2006). However, it is not always possible to carry out such experiments. They require permanent areas where one can establish long-term field experiments. Regrettably, there are not protected areas or biological stations covering the semi-arid zones in the Venezuelan Andes. The alternative is an observational approach in which the spatial distribution of potential nursed cacti in relation to plant cover produced by dominant shrubs is considered (*sensu* López *et al*. 2007). A higher concentration of cacti below shrubs is usually accepted as an indication of the nurse syndrome. Although other mechanisms could explain this pattern, such as differential seed rain among others, a study of correlative nature is the first step to evaluate the possible effect of dominant shrubs on the spatial distribution of cacti and other life forms.

In this work, the spatial associations between two globose cacti, *Mammillaria mammillaris* (L) Karsten and *Melocactus schatzlii* Till & Gruber, and two mimosoid shrubs, *Acacia farnesiana* (Willd.) L. and *Prosopis julifora* DC., were evaluated in the Lagunillas enclave, to determine the importance of the so-called nurse plant phenomenon for recruitment of both cacti. Two questions were addressed: 1) Is there greater spatial association between globose cacti and mimosoid legumes than expected by chance? 2) Does the relative importance of mimosoid shrubs as benefactor plants change between a cactus thicket and a thornscrub?

METHODS

Study site

This study was carried out from June to July 2006 in the Lagunillas semi-arid enclave in the Venezuelan Andes (262 km^2, Soriano and Ruíz 2002). Annual rainfall ranges from 450-550 mm, with peaks in April-May and September-October. Weather is semi-arid and is characterized by a warm climate with 22°C of mean annual temperature. The dominant vegetative elements

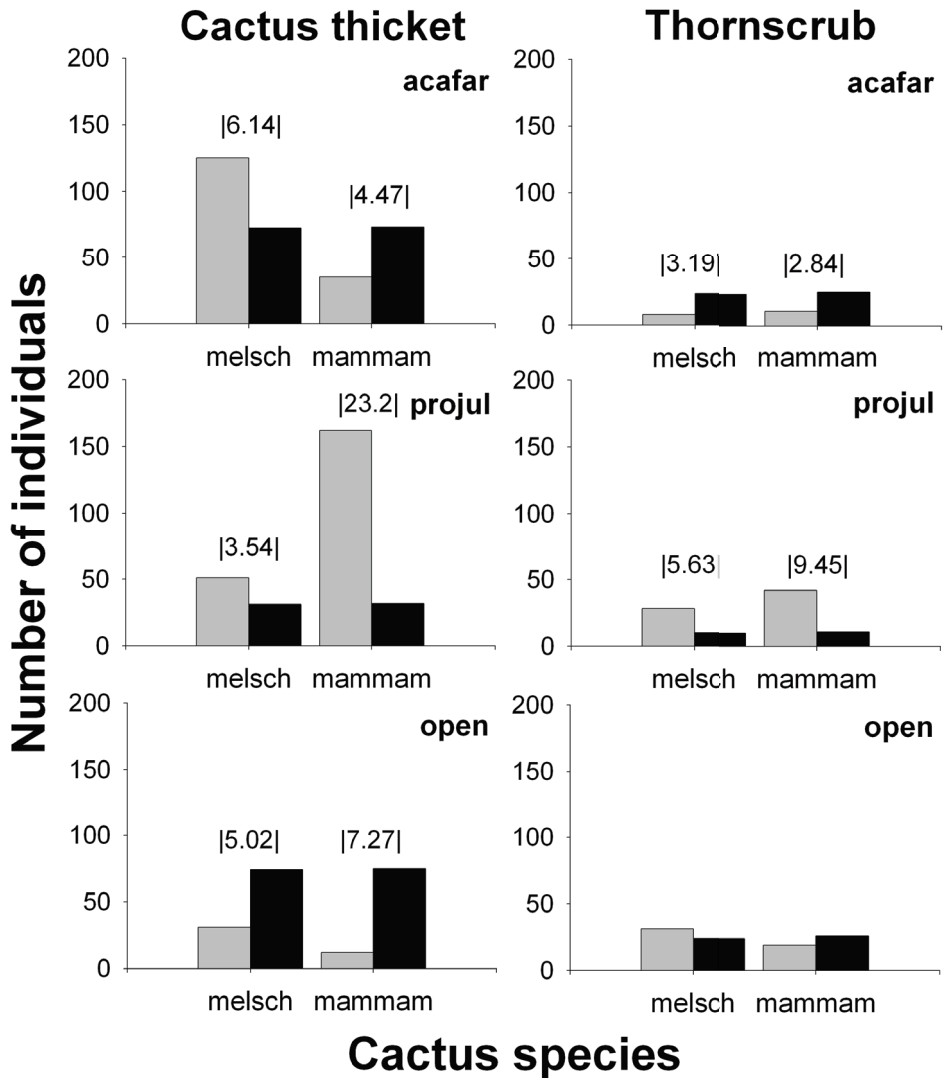

Figure 1. Observed (*grey bars*) and expected (*black bars*) number of *Melocactus schatzlii* (melsch) and *Mammilaria mammilaris* (mammam) growing below *Acacia farnesiana* (**acafar**), *Prosopis juliflor*a (**projul**) and open areas (**open**) in two contrasting habitat of the Lagunillas semi-arid enclave, Venezuela. Absolute values shown are significant at 5% of the normal distribution (standardized residuals test).

are mimosoid shrubs, such as *Prosopis juliflora* DC., *Acacia farnesiana* (Willd.) L. and *A. macracantha* H.B.K.; and columnar cactus species, such as *Stenocereus griseus* (Haw.) F. Busxb., *Cereus repandus* (L.) Backeb. and *Pilosocereus tillianus* Gruber & Schaftzl. In the lower stratum, together with small perennial and ephemeral plant species, the vegetation is characterized by the presence of globose cacti of the genus *Mammillaria* and *Melocactus*. Among these, *M. mammillaris* (L) Karsten and *M. schatzlii* Till & Gruber are the most abundant. Thornscrubs are strongly associated with small persistent water bodies of the enclave and contain high abundances of *P. juliflora* (~ 307 ind/ha), as well as scarce portions of bare areas (< 20%); while cactus thickets occur mainly on dry uplands and contain high abundance of *A. farnesiana* (~ 116 ind/ha), together with large portions of bare areas (30 - 35%) (Larrea-Alcázar and Soriano 2008). Both habitats can represent 62% (cactus thicket) and 28% (thornscrub) of the total cover

Table 1. Mean (± SE) and minimum-maximum size (diameter, cm) of *Melocactus schatzlii* and *Mammillaria mammillaris* beneath *Acacia farnesiana* and *Prosopis juliflora* and open areas in two habitats of a Venezuelan Andean dry valley.

Site and cactus species	**Mimosoid legume species and open areas**					
	Acacia farnesiana		*Prosopis juliflora*		Open areas	
CACTUS THICKET	Mean	Min-Max	Mean	Min-Max	Mean	Min-Max
Melocactus schatzlii	10.6	2.5 – 21.5	10.9	2.5 – 17	12.3	4 – 18
(*n* = 202)	(0.35)		(0.49)		(0.48)	
Mammilaria mammillaris	4.6	2.5 – 7	4.9	1.7 – 8	4.7	2.5 – 8
(*n* = 209)	(0.24)		(0.1)		(0.38)	
THORNSCRUB	Mean	Min-Max	Mean	Min-Max	Mean	Min-Max
Melocactus schatzlii	12.1	8 – 14	12.7	8 – 16.5	11.4	3 – 15
(*n* = 67)	(0.69)		(0.33)		(0.51)	
Mammilaria mammillaris	4.4	3 – 6	4.5	2 – 6.5	4.5	3 – 7.5
(*n* = 72)	(0.24)		(0.15)		(0.3)	

of the enclave (Rico *et al*. 1996) and there is no difference in annual rainfall between them. Grazing and removal of taller thorny legumes have increased the processes of erosion and desertification in both habitats and the natural vegetation is being slowly replaced by cultivation and by high-intensity grazing by cows and goats. The study was conducted in two study sites within the enclave. The former was located close to Caparú Lagoon (8º29'17'' N and 71º20'16'' W), 3 km South-East of San Juan de Lagunillas, Mérida State, at an altitude of 780 m. This site was defined as low thornscrub in which long-lived mimosoid shrubs form a discontinuous thorny landscape and is located 0.6-0.7 km from the lagoon. The second site was located near San Juan de Lagunillas town (8º30'10'' N and 71º21'53'' W), at an altitude of 990 m. This site was defined as interrupted cactus thicket which contains a high abundance of columnar cacti as well as high portions of open areas resulting in a dry landscape strongly dominated by cacti. These sites were separated from one another by approximately 8-10 km. Both sites contain large populations of *M. schatzlii* and *M. mammillaris* compared to other sites within the enclave, making them appropriate for conducting this study. In the following sections mimosoid shrubs (*P. juliflora* and *A. farnesiana*) and globose cacti (*M. schatzlii* and *M. mammillaris*) will be referred to only by the genus name.

Spatial association assessment

To examine the relative spatial association between globose cacti and mimosoid shrubs at both sites, mature individuals of *Acacia* (cactus thicket: 18 ind; thornscrub: 8 ind) and *Prosopis* (cactus thicket: 14 ind; thornscrub: 18 ind) were selected. Individuals with partially or completely isolated canopies were selected in order to avoid the influence of adjacent neighbors. Below the crown of each shrub, a 50-cm wide transect that covered the diameter of the canopy (shrub-covered area) and an area of similar size in an adjacent open area of the focal shrub (control area) were established. Open areas were considered as the control situations, which were areas completely lacking vegetation. The

orientation of each 50-cm wide transect was fixed in a North-South direction to avoid sampling bias as some species could establish in some position or fail to show orientation preferences. Because each radius varied in length, to compare canopies radii were divided into five standard segments (0 to 20, 21 to 40, 41 to 60, 61 to 80 and 81-100%), which corresponded to the proportional distance from the shrub's trunk to the edge of the canopy (Mandujano *et al*. 2002). The adjacent open areas were subdivided into similar segments. These field measures did not allow us to avoid the effect of canopy size on the counted number of cacti. Tall shrubs would have higher environment heterogeneity compared with small shrubs and, thus, the former would likely harbour a high number of nursed cacti. However, these measures allow to compare the establishment of both globose cacti between shrub-covered and open areas (control). Abundance, species and location of globose cacti, including diameter (cm) and conservation status (trampled/untouched) of each plant, were recorded. The individuals of *Melocactus* and *Mammillaria* were classified into four diameter classes (1-6, 7-12, 13-18 and 19-24 cm) to explore the existence of better microsite conditions beneath both mimosoid plants as compared to open areas. To determine if globose cacti were randomly distributed among both perennial plants, published data on the cover of both mimosoid species were used (Larrea-Alcázar and Soriano 2008).

Data analysis

Separate Chi-square tests (χ^2) were used to test the null hypothesis that the number of globose cacti under each perennial plant is proportional to the total area covered by the canopy of each mimosoid shrub. The ratio between observed and expected number of globose cacti was also calculated to establish an association index between both values (*sensu* Drezner 2006). Separate standardized residuals tests were used to assess the significance of each cell, assuming that any value greater than two was regarded as a significant deviation (Greig-Smith 1983).

Separate unidirectional Kolmogorov-Smirnov two-sample tests ($D_{m,n}$) were conducted to evaluate differences in the abundance of globose cacti beneath mimosoid shrubs and open areas in relation to the five standardised distances from the shrub's trunk to the edge of the canopy. The $D_{m,n}$ is equal to $max\ |S_m\ (X) - S_n\ (X)|$, where $S_m\ (X)$ is the observed frequency distribution of cacti under a shrub species m and $S_n\ (X)$ is the accumulated relative distribution of globose cacti in open areas n (Siegel and Castellan 1995). Significance of observed $D_{m,n}$ was estimated sing the relationship $\chi^2 = 4D^2_{m,n}\ (mn/m+n)$, which is near to a χ^2 distribution with df = 2 (Goodman 1954). In all cases, a 0.05 rejection level was used.

Finally, separate Chi-square tests (χ^2) were carried out to test the null hypothesis that the number of globose cacti is similar for the four diameter classes. This was defined to explore the existence of better microsites beneath both mimosoid shrubs. If shrub-covered areas have a

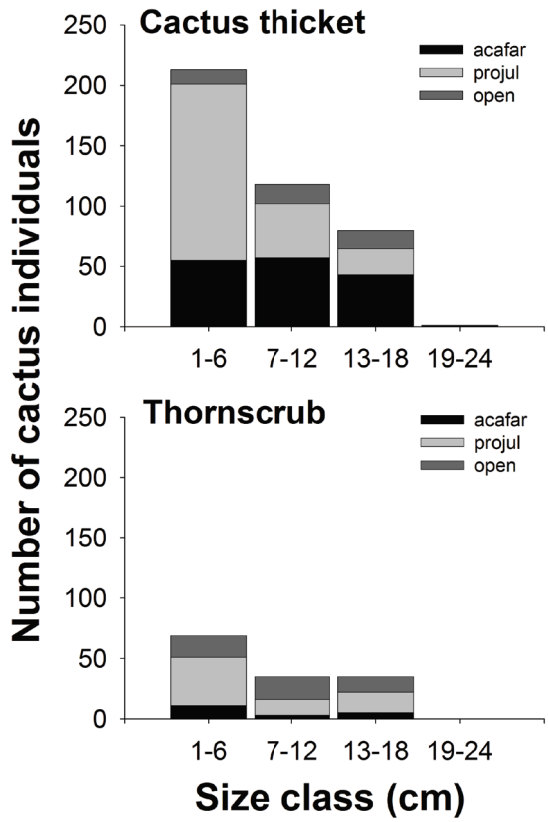

Figure 2. Total number of globose cacti belonging to four different size classes growing under *Acacia farnesiana* (**acafar**), *Prosopis juliflora* (**projul**) and bare areas (**open**) in a cactus thicket (a) and a thornscrub (b) of the Lagunillas semi-arid enclave, Venezuela.

better quality habitat than unshaded spaces (open areas), they can increase recruitment success, i.e., contain a high number of cacti, or they can increase growth and individual fitness, i.e., contain a high number of large cacti (or older cacti). The package Statistica (version 6.0) was used for all analyses (StatSoft Inc. 2001).

RESULTS

Spatial association assessment

Overall, 457 individuals of *Melocactus* and *Mammillaria* were found below isolated individuals of *Acacia* (174 ind, 31.6%) and *Prosopis* (283 ind, 51.4%). Moreover, 93 globose cacti were only found in open areas (16.9%).

In the cactus thicket, the number of globose cacti below both mimosoid shrubs was significantly higher than that expected by chance (χ^2 = 688.8, d.f = 2, $p < 0.0001$). Comparison of observed and expected numbers shows *Melocactus* individuals strongly associated with *Acacia* ($Ratio_{obs/exp}$ = 1.72; Standardized Residuals Test = |6.14|) and *Prosopis* shrubs ($Ratio_{obs/exp}$ = 1.63; Standardized Residuals Test = |3.54|), while *Mammillaria* individuals were only related to *Prosopi*s shrubs ($Ratio_{obs/exp}$ = 5.14, Standardized residuals tests = |23.2|, Figure 1). The number of globose cacti present in open areas was not significantly higher than that expected by chance (absolute values < 2, Figure 1) and damaged individuals by trampling were not found in any of the mesohabitats (shrub-covered and open areas).

In the thornscrub, the number of globose cacti under canopies of both mimosoid shrubs was also significantly higher than that expected by chance (χ^2 = 143.2, d.f = 2, $p < 0.0001$). Comparison of observed and expected number shows *Melocactus* and *Mammillaria* to be associated to *Prosopis* shrubs ($Ratio_{obs/exp}$ = 2.77 and 3.87; Standardized residuals tests = |5.63| and |9.45|, respectively). In contrast, the number of globose cacti beneath shrubs of *Acacia* and open areas was not significantly higher than expected by chance (absolute values < 2, Figure 1). Damaged cacti of *Melocactus* were not recorded in any of the mesohabitats. In contrast, beneath *Prosopis* canopies, the proportion of damaged *Mammillaria* cacti was significantly higher (73.8%) than that of untouched cacti (26.2%) (proportion test, $p <$ 0.0001), while below *Acacia* canopies and open areas, the proportion of damaged and untouched cacti was not significantly different (proportion test, $p = 0.68$ and $p = 0.34$, respectively).

In the cactus thicket, analysis of differences in the abundance of globose cacti in relation to distance from the shrub's trunk and open areas shows that the observed distribution of *Mammillaria* beneath *Acacia* and *Prosopis* shrubs was significantly higher than the accumulated distribution of cacti in open areas (χ^2 = 14.8 and χ^2 =35.3, respectively, with d.f = 2 and $p < 0.0001$ in both cases). Below *Acacia* shrubs, a higher deviation of the accumulated distributions at medium distances with respect to the main trunk was found (21-40%, $D_{m,n}$ = |0.43|), while below *Prosopis* shrubs, the value of higher deviation was recorded near the edge of the canopy (61-80%, $D_{m,n}$ = |0.66|). In the thornscrub, the accumulated distribution of *Melocactus* under *Prosopis* shrubs was significantly higher in relation to the observed frequency distribution in open areas (χ^2 = 16.9, d.f = 2, $p < 0.0001$), where the higher deviation value was found at medium distances with respect to the main trunk (41-60%, $D_{m,n}$ = |0.5|).

On the other hand, at both sites the average size (diameter) of *Melocactus* and *Mammillaria* beneath mimosoid shrubs canopies did not differ from that of cacti established in open areas (Table 1). In the cactus thicket, analysis of total number of both cactus species belonging to the four different sizes showed a high presence of individuals of the 1-6 cm diameter class underneath *Prosopis*, as compared with open areas showing a high presence of *Mammillaria* individuals of this size category (χ^2 = 54.6, d.f = 6, $p < 0.0001$, Figure 2a). The thornscrub, however, showed that the total number of cacti for all sizes was not independent of what we would have expected by chance (χ^2 = 8.1, d.f = 6, $P = 0.25$, Figure 2b).

DISCUSSION

The shaded canopies of both mimosoid bushes seem to have an important effect on the spatial distribution of both globose cacti. However, this positive impact would depend of the cactus or shrub species and the site (cactus thicket or thornscrub). Individuals of *Melocactus* were found associated to both mimosoid shrubs in the two sites, while individuals of *Mammillaria* were only related to *Prosopis* (see Figure 1). This spatial pattern has also been shown for other

growth forms of cacti in the Lagunillas enclave (Larrea-Alcázar and Soriano 2008), showing that establishment and recruitment of many cactus species may take place in shrub-covered areas. Nevertheless, the presence of cacti established in open areas shows that establishment of globose cacti in this Andean semi-desert enclave does not necessarily depend on nurse associations. This result implies that these globose cacti are capable for establishment in open areas. This topic has been suggested by several authors (Rodriguez 1998, Nobel *et al*. 1986, 1992) and strongly supports the hypothesis that the need of a nurse plant for establishment of some globose cacti is highly facultative (Mandujano *et al*. 2002, Godínez-Álvarez *et al*. 2003, López and Valdivia 2007). Some rocks, several surface irregularities or herbs may act as potential or ephemeral facilitators allowing germination and seedling survival (Nobel *et al*. 1986, Godínez-Álvarez *et al*. 2003, Munguía-Rosas and Sosa 2008, Peters *et al*. 2008).

Many cactus species are known to require the more mesic conditions below shrubs in order to get established (Franco and Nobel 1989, Valiente-Banuet and Ezcurra 1991, Valiente-Banuet et al. 1991, Suzán et al. 1996, Reyes-Olivas et al. 2002). Both cactus species showed an unimodal distribution below the canopies of both mimosoid shrubs, with high frequency distributions at medium distances with respect to the main trunk (*Acacia:* 21-40%; *Prosopis*: 41-60%). The ability of both mimosoid legumes to retain their leaves for a long time, together with their capacity to modify the light intensity and soil properties underneath their crown, may partially explain these results. This mechanism has been suggested to other nurse shrub species (*Prosopis flexuosa*, Rossi and Villagra 2003). However, other mechanisms may also be regulating the spatial arrangement of nursed globose cacti under both dominant perennial plants. For instance, the presence of allelochemicals in the stems, leaves or roots of both mimosoid plants may affect the distribution of cacti beneath their crowns. In fact, aqueous extracts obtained from leaves, fruits and seeds of *Prosopis* inhibit the radicle growth of many grass species (Nakano *et al.* 2004, Goel *et al.* 2005). Their effects on germination, growth, survival and spatial arrangement of cacti occurring below the canopies of these shrubs are unknown.

In the cactus thicket, differences in size distribution between the established cacti protected below the canopy of mimosoid bushes (mainly beneath *Prosopis*) and those in open areas were found (see Figure 2). This suggests that in a water stressed habitat, both cacti (mainly *Mammillaria*) would accumulate more biomass (or older individuals) under shaded conditions than in open areas (*sensu* Martínez-Berdeja and Valverde 2008). However, it is very well known that some cactus can have the same biomass but allocated in a different form (Godínez-Álvarez *et al.* 2003, Drezner and Lazarus 2008). For instance, two individuals may have the same biomass but the individual that allocated more to belowground structures will have a lower stature (or diameter) above ground compared to other that allocated less to belowground structures. This topic was not evaluated in this work and should be part of a future research. Likewise, the overrepresentation of individuals in the 1 to 6 cm category may also be a consequence of accumulated success of establishment over several years or be the result of differential mortality or growth rates below the canopy of benefactor plants compared to open areas (Mandujano *et al.* 2002).

On the other hand, in the thornscrub, 73.8% of *Mammillaria* individuals below *Prosopis* canopies had signs of damage due to trampling. This process has been operating for years in the Lagunillas enclave; however, its effects on spatial distribution of globose cacti are little documented. Strong physical damage by trampling may be critical for the natural regeneration of *Mammillaria*. Goats and cows use the canopies of both mimosoid shrubs as shade resource in order to avoid the high temperatures that occur in this harsh environment. Although the presence of these domestic mammals appears to affect the spatial distribution of this globose cactus, this conclusion needs experimental corroboration.

In summary, regardless of the precise mechanisms that may allow the establishment of both globose cacti below the canopies of both mimosoid shrubs and in open areas, the results show that both dominant shrubs seem to affect the spatial distribution of both globose cacti. Several studies from different semi-arid ecosystems have reported spatial relationships between perennial bushes and cacti with different growth forms (see Godínez-Álvarez *et al.* 2003, Flores and Jurado

2003, Drezner and Lazarus 2008). This is the first study reporting a positive plant-plant spatial association between globose cacti and mimosoid shrub species from a semi-arid desert in the Andes of northern South America. Given the correlative nature and restrictions of the field technique used in our study there is a need for future demographic and ecological studies to examine recruitment and establishment of both cactus species over long time periods. Nevertheless, this study provides a foundation for future research and essential information to increase our knowledge on the role of mimosoid plants as nurse plants in the tropical Andes.

ACKNOWLEDGEMENTS

Assistance in the field sampling was provided by A.J. Pérez and C. Arangüren. J. Nassar and R.P. López made valuable comments and suggestions on the manuscript. The work was supported by The Rufford Small Grant for Nature Conservation (RSG, Grant 17.01.06), the Red Latinoamericana de Botánica- Tyler Prize 2004 (Grant RLB-02-D2), and the Consejo de Desarrollo Científico, Humanístico y Tecnológico of the Universidad de Los Andes (CDCHT-ULA, Grant C-1306-05-01-ED). This support is gratefully acknowledged.

LITERATURE CITED

DE VIANA M.L., SUHRING, S. and B. MANLY. 2001. Application of randomization methods to study the association of Trichocereus pasacana (Cactaceae) with potential nurse plants. Plant Ecology 156: 193-197.

DREZNER, T.D. 2006. Plant facilitation in extreme environments: The non-random distribution of saguaro cacti (Carnegiea gigantea) under their nurse associates and the relationship to nurse architecture. Journal of Arid Environments 65: 46-61.

DREZNER, T.D. and B.L. LAZARUS. 2008. The population dynamics of columnar and other cacti: a review. Geography Compass 2: 1-29.

FLORES, J. and E. JURADO. 2003. Are nurse-protégé interactions more common among plants from arid environments?. Journal of Vegetation Science 14: 911-916.

FRANCO, A.C. and P.S. NOBEL. 1989. Effect of nurse plants on the microhabitat and growth of cacti. Journal of Ecology 77: 870-886.

GODÍNEZ-ÁLVAREZ, H., VALVERDE, T. and P. ORTEGA-BAES. 2003. Demographic trends in the Cactaceae. Botanical Review 69: 173-203.

GOEL, U., SAXENA B. and B. KUMAR. 2005. Comparative study of allelopathy as exhibited by Prosopis juliflora Swarts and Prosopis cineraria (L) Druce. Journal of Chemical Ecology 15: 591-600.

GOODMAN, L.A. 1954. Kolmogorov-Smirnov tests for psychological research. Psychological Bulletin 51: 160-168.

GREIG-SMITH, P. 1983. Quantitative Plant Ecology. UK: Blackwell, Oxford.

LARREA-ALCÁZAR, D.M. and P.J. SORIANO. 2008. Columnar cacti-shrub relationships in an Andean semiarid valley in western Venezuela. Plant Ecology 196: 153-161.

LÓPEZ, R.P., VALDIVIA, S., SANJINÉS, N. and D. DE LA QUINTANA. 2007. The role of nurse plants in the establishment of shrub seedlings in the semi-arid subtropical Andes. Oecologia 152: 779-790.

LÓPEZ, R.P. and S. VALDIVIA. 2007. The importante of shrub cover for four cactus species differing in growth form in an Andean semi-desert. Journal of Vegetation Science 18: 263-270.

MANDUJANO, M.C., FLORES-MARTÍNEZ, A., GOLUBOV J. and E. EZCURRA. 2002. Spatial distribution of three globose cacti in relation to different nurse-plant canopies and bare areas. Southwestern Naturalist 47: 162-168.

MARTÍNEZ-BERDEJA, A. and T. VARVERDE. 2008. Growth responde of three globose cacti to radiation and soil moisture: An experimental test of the mechanism behind the nurse effect. Journal of Arid Environments 72: 1766-1774.

MUNGUÍA-ROSAS, M.A. and V.J. SOSA. 2008. Nurse plants vs. nurse objects: effects of woody plants and rocky cavities on the recruitment of the Pilosocereus leucocephalus columnar cactus. Annals of Botany 101: 175-185.

NAKANO, H., NAKAJIMA E., FUJII Y., AMADA K., SHIGEMORI H. and K HASEGAWA. 2004. Leaching of the allelopathic substance, -tryptophan from the foliage of mesquite (Prosopis juliflora (Sw.) DC.) plants by water spraying. Plant and Growth Regulation 40: 49-52.

NOBEL, P.S., GELLER, G.N.; KEF S.C. and A.D. ZIMMERMAN. 1986. Temperatures and thermal tolerances for cacti exposed to high temperatures near sol surface. Plant, Cell and Environment 9: 279-287.

NOBEL, P.S., MILLER, P.M. and E.A. GRAHAM. 1992. Influence of rocks on soil temperature, soil water potential, and rooting patterns for desert succulents. Oecologia 92: 90-96.

PETERS, E.M., MARTOLL, C. and E. EZCURRA. 2008. Nurse rocks are more important than nurse plants in determining the distribution and establishment of globose cacti (Mammillaria) in the Tehuacán Valley, Mexico. Journal of Arid Environments 72: 593-601.

REYES-OLIVAS, A., GARCÍA-MOYA, E. and L. LÓPEZ-MATA. 2002. Cacti-shurb interactions in the coastal desert of northern Sinaloa, Mexico. Journal of Arid Environments 52: 431-445.

RICO, R., RODRÍGUEZ, L.E., PÉREZ, R. and A. VALERO. 1996. Mapa y análisis de la vegetación xerófila de las lagunas de Caparú, cuenca media del río Chama, Estado Mérida. Plántula 1: 83-94.

RODRÍGUEZ, C. 1998. ¿Explica la morfología de la cubierta de espinas la distribución del hábitat de algunas especies de cactáceas?: los casos de Mammillaria pectinifera y M. carnea en el valle de Zapotitlán Salinas, Puebla. BSc thesis. Universidad Nacional Autónoma de México, UNAM, México D.F.

ROSSI, B.E. and P.E. VILLAGRA. 2003. Effects of Prosopis flexuosa on soil properties and the spatial pattern of understory species in arid Argentina. Journal of Vegetation Science 14: 543-550.

SARMIENTO, G. 1972. Ecological and floristic convergences between seasonal plant formations of tropical and subtropical South America. Journal of Ecology 60: 367-410.

SIEGEL, S. and N.J. CASTELLAN. 1995. Nonparametric Statistics for the Behavioral Sciences. McGraw-Book Company, New York.

SORIANO, P.J. and A. RUÍZ. 2002. The role of bats and birds in the reproduction of columnar cacti in the Northern Andes. Pp. 241-263.In: Fleming, T.H. & A. Valiente-Banuet (eds.). Evolution, ecology and conservation of columnar cacti and their mutualists. Arizona University Press, Tucson.

STATSOFT, Inc. 2001. STATISTICA (data analysis software system), version 6. www.statsoft.com.

SUZÁN, H., NABHAN, G.P. and D.T. PATTERN. 1996. The importance of Olneya tesota as nurse plant in the Sonoran Desert. Journal of Vegetation Science 7: 635-644.

SUZÁN-AZPIRI, H. and V.J. SOSA. 2006. Comparative performance of the giant cardon cactus (Pachycereus pringlei) seedlings under two leguminous nurse plant species. Journal of Arid Environments 65: 351-362.

TEWSBURY, J.J. and J.D. LLOYD. 2001. Positive interactions under nurse-plants: spatial scale, stress gradients and benefactor size. Oecologia 127: 425-434.

VALIENTE-BANUET, A. and E. EZCURRA. 1991. Shade as a cause of the association between the cactus Neobuxbaumia tetetzo and the nurse plant Mimosa luisana in the Tehuacán Valley, Mexico. Journal of Ecology 79: 961-971.

VALIENTE-BANUET, A., VITE F. and J.A. ZAVALA-HURTADO. 1991. Interaction between the cactus Neobuxmaumia tetetzo and the nurse shrub Mimosa luisana. Journal of Vegetation Science 2: 11-14.

Recibido 2 de octubre de 2008; revisado 13 de enero de 2009; aceptado 20 de febrero de 2009