UNIVERSIDAD DE CHILE - FACULTAD DE CIENCIAS - ESCUELA DE PREGRADO

PATRÓN DE RECLUTAMIENTO, CRECIMIENTO Y SOBREVIVENCIA DE DOS ESPECIES DE CACTÁCEAS COLUMNARES EN CHILE SEMIÁRIDO

Seminario de Título entregado a la Universidad de Chile en cumplimiento parcial de los requisitos para optar al Título de Biólogo con mención en Medio Ambiente

ROCÍO ANDREA CARES SUÁREZ

Director de Seminario de Título: Dra. Carezza Botto

Co- Director de Seminario de Título: Dr. Rodrigo Medel

Marzo, 2012

Santiago – Chile

INFORME DE APROBACIÓN SEMINARIO DE TITULO

Se informa a la Escuela de Pregrado, Facultad de Ciencias, Universidad de Chile que el Seminario de Título, presentado por la Srta. Rocío Andrea Cares Suárez

"Patrón de reclutamiento, crecimiento y sobrevivencia de dos cactáceas columnares en Chile semiárido"

Ha sido aprobado por la Comisión de Evaluación, en cumplimiento parcial de los requisitos para optar al Título de Biólogo con mención en Medio Ambiente.

Dra. Carezza Botto
Director Seminario de Título

Dr. Rodrigo Medel
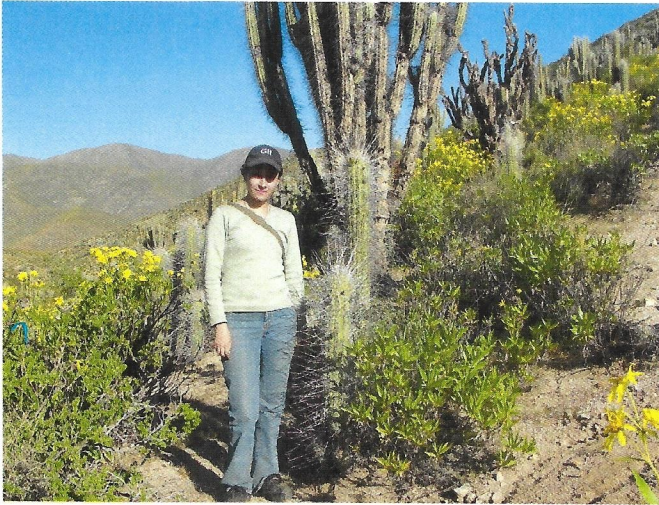**Co-Director Seminario de Título**

Comisión de Evaluación

Dr. Ramiro Bustamante
Presidente Comisión

Dr. Pablo Guerrero
Evaluador

Santiago de Chile, Marzo de 2012.

BIOGRAFÍA

Nació en la cuidad de La Serena y vivió sus primeros años en la comuna de Vicuña (Región de Coquimbo). A los cuatro años se trasladó a Santiago, en donde comenzó sus estudios de enseñanza básica en el London College. Posteriormente, entró a estudiar al Centro Educacional La Florida hasta completar la enseñanza media.

Hija de un artesano y una dueña de casa, desde pequeña siempre le interesaron las ciencias naturales, en especial las ciencias de la tierra. Cuando estaba en la enseñanza media, soñaba con ser sismóloga y dedicarse a estudiar los movimientos telúricos. Pero la vida la llevaría por otro camino y en el 2006 entró a estudiar Biología ambiental en la Universidad de Chile, siendo su principal objetivo la conservación del medio ambiente. Durante el cuarto año de carrera, entró a trabajar en el laboratorio de Ecología Evolutiva con la Dra. Botto y desde entonces, ha dedicado gran parte de sus estudios a la ecología de cactáceas. A lo largo de estos años, ha demostrado gran perseverancia, esfuerzo y compromiso con los desafíos que le ha tocado enfrentar.

Finalmente, sólo me resta decir, que durante todo este tiempo ha sido la mejor hermana y amiga que pude haber deseado tener.

Roxana

"Cuando hayas cortado el último árbol,
contaminado el último río,
y pescado el último pez,
te darás cuenta que el dinero no se puede comer"

Proverbio indio.

CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDICES

RESUMEN

La medida en la cual el reclutamiento de cactáceas es influenciado por factores bióticos y abióticos es una pregunta relevante en ecología de ambientes desérticos, pues permite conocer los determinantes que restringen la mantención y viabilidad de poblaciones naturales. En este estudio, se examinaron los patrones de reclutamiento de *Echinopsis chiloensis* y *Eulychnia acida,* dos cactus columnares endémicos que habitan las zonas semiáridas de Chile. Específicamente, el estudio se realizó en la Reserva Nacional Las Chinchillas, ubicada a ~300 km al noreste de Santiago, Chile. Se determinó el crecimiento y sobrevivencia de juveniles (<30 cm de altura) mediante monitoreos semestrales entre los años 2009 - 2011 en dos microhábitats contrastantes en sus variables abióticas (bajo arbusto y en suelo desnudo). Se determinó el número de individuos juveniles presentes en ambos microhábitats y se evaluó la potencial asociación de éstos con plantas nodrizas identificando la especie de arbusto bajo la cual se encontraban los juveniles. Cada microhábitat fue caracterizado por su temperatura mínima, máxima y promedio, humedad relativa, contenido hídrico y características físicas y químicas del suelo. Los resultados indican que la mayoría de los cactus juveniles se encuentran bajo arbusto, donde se registraron las temperaturas máxima y promedio más bajas. En general, se observó una mayor ocurrencia de *E. chiloensis* y *E. acida* bajo las especies arbustivas *Flourensia thurifera* y *Bahia ambrosioides*, respectivamente, que lo esperado por su abundancia relativa en el campo. Esto sugiere que ambas especies de arbusto podrían estar actuando como nodrizas mediante un efecto especie-específico.

Palabras clave: Cactácea, planta nodriza, cactus juvenil, *Echinopsis*, *Eulychnia.*

ABSTRACT

The extent to which cactus recruitment is influenced by biotic or abiotic factors is a relevant question in ecology of arid environments because it gives insights about the restrictions on the maintenance and viability of natural populations. In this study, I examined the pattern of recruitment of *Echinopsis chiloensis* and *Eulychnia acida*, two endemic columnar cacti that inhabit the arid and semiarid zones of Chile. Specifically, the study was carried out at the Reserva Nacional Las Chinchillas, located at ~300 km north from Santiago, Chile. I determined growth and survivorship of young cacti (<30 cm height) through biannual monitoring between 2009-2011 in two microhabitats that strongly differ in their abiotic variables (under shrub and bare soil). I determined the number of young cacti occurring in sheltered and open microhabitat and examined the potential association of these with nurse plants identifying the shrub species where juveniles occurred. Each microhabitat was characterized by their minimum and maximum temperature and mean relative humidity, hydric content, and physical and chemical soil characteristics. Results indicate that most young cacti occurred under shrubs, where I recorded the lower mean and maximum temperatures. Overall, I detected a higher occurrence of *E. chiloensis* and *E. acida* under the shrub species *Flourensia thurifera* and *Bahia ambrosioides*, respectively, than the random expectation based on these shrub relative abundances in the field. This suggests that both species of shrub could acts as a nurse by a species-specific effect.

Keywords: Cactaceae, nurse plant, young cacti, *Echinopsis*, *Eulychnia*.

INTRODUCTION

The local abundance of cactus populations is conditioned in a large extent by seed germination and seedling survival (Godínez-Álvarez et al., 2003). During the early stages of the life-cycle, seedlings are often exposed to extreme environmental conditions such as drought, hot soils, and low moisture content which turns this stage to one of the most critical to maintain viable populations (Valiente-Banuet and Ezcurra, 1991). However, other factors such as the more frequent establishment of seedlings under the canopy of other plant species (Flores and Jurado, 2003) may counteract the negative effect imposed by desiccation and high soil temperatures. Several studies have reported that nurse plants are important for seedling establishment and cactus recruitment (Turner et al., 1966; Franco and Nobel, 1989; Valiente-Banuet and Ezcurra, 1991; Mandujano et al., 1998, see review in Rojas-Aréchiga and Vázquez-Yanes, 2000). Nurse plant effects may occur through diverse mechanisms such as (i) protection against direct solar radiation (Valiente-Banuet et al., 1991b, Valiente-Banuet et al., 2002), (ii) reduction of daytime high soil surface temperatures (Franco and Nobel, 1989), (iii) reduction of night-time and winter heat loss beneath their canopy (Nobel, 1980), (iv) reduction of wind (Drezner, 2006), (v) addition of nutrients to the soil (Franco and Nobel, 1989), and (vi) protection against herbivores (Muro et al., 2011).

While the importance of nurse plants for cactus recruitment has been mostly evaluated in the arid zones of North America (see review in Godínez-Álvarez et al., 2003; Suzán-Azpiri and Sosa, 2006), and other regions of the world (Valiente-Banuet et al., 1991a), there is a conspicuous lack of knowledge of this phenomenon for South American

cacti. Examples of this association in other parts of the world are (i) the cactus *Carnegiea gigantea* (Engelm) Britton and Rose (Cactaceae) and its nurse plants *Ambrosia deltoidea* Torr. (Asteraceae), *Cercidium microphyllum* (Torr.) Rose and I. M. Johnst (Fabaceae), *Encelia farinosa* Torr. and A. Gray (Asteraceae), *Larrea tridentata* (DC) Coville (Zygophyllaceae), *Olneya tesota* A. Gray (Fabaceae) and *Prosopis juliflora* (Sw) DC (Fabaceae), which offer shade (Turner et al., 1966), frost protection (Hutto et al., 1986) and predation avoidance (Franco and Nobel, 1989), and (ii) the cactus *Neobuxbaumia tetetzo* (Coulter) Backeberg (Cactaceae) with *Mimosa luisana* Brandegee (Mimosaceae) as nurse plant, which offers shade (Valiente-Banuet and Ezcurra, 1991) and increases soil nutrients (Carrillo-García et al., 2000).

The columnar cactus species richness of Chilean arid and semiarid zones is relatively low compared to Mexico and Argentina (Ortega-Baes and Godínez-Álvarez, 2006), being *Echinopsis* and *Eulychnia* the most diversified genera (Hoffmann and Walter, 2004; Medel et al., 2010). *Echinopsis chiloensis* and *Eulychnia acida* are two widely distributed endemic columnar species that inhabit mainly north-facing slopes in semiarid Chile (Medel, 2000). Currently, the two species do not present important conservation problems (Hoffmann and Walter, 2004), being categorized as of "least concern" according to Hunt (2006). However, human-induced disturbance such as logging and replacement of native habitats by agricultural and pasture areas might threaten their current conservation status. According to Ortega-Baes and Godínez-Álvarez (2006), Chile has the highest proportion of endemic cactus species, which translates into a high overall richness and number of endemic species than expected according to its area.

In this study, I examine the role of shrub species on the recruitment of *E. chiloensis*

and *E. acida*. More specifically, I will attempt to answer the following questions: (i) Do shrub species act as nurse plants of *E. chiloensis* and *E. acida*? (ii) Does each cactus species differ in the shrub species used as potential nurse plants? In addition, it is possible to address a comparative question such as: (iii) Do cactus species exhibit similar responses to the association with nurse plants?

MATERIALS AND METHODS

2.1. Study site and natural history

This study was carried out at the Reserva Nacional Las Chichillas (31° 30' S, 71° 06' W), a protected area located ~300 km northeast from Santiago and 60 km east from the Pacific coast. The climate of the study site is of a semiarid Mediterranean-type with most rainfall concentrated between June and August (di Castri and Hajek, 1976). Mean annual precipitation is 185.0 mm with ample variation across years, alternating long droughts and unusual years of high rainfall seemingly associated to El Niño events (di Castri and Hajek, 1976). Vegetation forms are thorn scrub, thorn and sclerophyllous forest (Luebert and Pliscoff, 2006), and is mainly represented by *F. thurifera* (Mol.) DC (Asteraceae), *B. ambrosioides* Lag. (Asteraceae), and *Porlieria chilensis* Johnst. (Zygophyllaceae) as the most common shrub species (Medel et al., 2004). The cactus species in the study site consist on the columnar *E. chiloensis* (colla) Fried. y Rowl. (Cactaceae) and *E. acida* Phil. (Cactaceae), and the spherical *Cumulopuntia sphaerica* (C.F.Först.) E.F. Anders. (Cactaceae) and *Eriosyce aurata* (Pfeiffer) Backeb. (Cactaceae) (Martínez del Río et al., 1995; Medel, 2000; Medel et al., 2002; Hoffmann and Walter, 2004).

E. chiloensis and E. acida (Fig. 1) are two endemic columnar cacti that inhabit in north-central Chile. Their reproduction is relatively synchronous with the blooming season extending from early September to mid-November, and the fruiting season from mid-October to late December or mid-January (Medel, 2000). *E. chiloensis* presents arborescent growth, of up to 8.0 m of height, generally very branched out or with several trunks going out near the base (Hoffmann, 1989). Areoles of *E. chiloensis* consist of 1–2 long central

Fig. 1. *Echinopsis chiloensis* (left) and *Eulychnia acida* (right)

sclerified spines that project outward and 8–12 short lateral spines that point in all directions (Medel, 2000). *E. acida* presents arborescent growth, from 1.5 to 4.0 m of height, very branched out, usually with only one trunk (Hoffmann, 1989). Areoles of *E. acida* consist of 1–2 long central spines and 10–13 short lateral spines (Medel, 2000). Scarce information has been reported about the growth pattern of columnar cacti, but Hoffmann (1989) suggests that natural regeneration may be difficult and growth rate extremely low.

2.2. Recruitment and height of young cacti

In May 2009, 205 and 104 reproductive cactus individuals of *E. chiloensis* and *E. acida*, respectively, were randomly chosen from north-facing slopes inside the study area. Individuals were distant at least 10 m one from each other. Each parental individual was delimited by a circumference of 10 m radius from the cactus base to record the number of young cacti of each species. I considered as young cacti to those individuals up to 30 cm of height. I quantified the height of each young cactus ($n = 171$) and its distance to the putative parental cactus with a tape (0.1 cm precision). The microhabitat where young cacti were found was categorized as: (i) sheltered microhabitat (SM), when the young cactus was under shrubs or parental cacti, or (ii) open microhabitat (OM), when the young cactus was in open bare soil. The recruitment was defined as the total number of young cacti found in both microhabitats. In addition, in the same north-facing slope, I set 10 line transects of 50 m each to estimate the relative microhabitat availability and the relative abundance of every shrub species presents in the study site including *Adesmia microphylla* Hook. and Arn. (Fabaceae), *B. ambrosioides*, *Bridgesia incisifolia* (Cambess) Bert. (Sapindaceae), *Cordia decandra* Hook. and Arn. (Boraginaceae), *Ephedra chilensis* K. Presl. (Ephedraceae), *F.*

thurifera, *Heliotropium stenophyllum* Hook. and Arn. (Boraginaceae), *Krameria cistoidea* Hook. and Arn. (Krameriaceae), *P. chilensis*, and *Senna cumingii* Hook. and Arn. (Fabaceae).

The height of young cacti was compared between species and microhabitats using a factorial ANOVA, and the distance of recruitment (i.e., the distance between a putative parental cactus and a young cactus) was compared using one-way ANOVA. All data were log-transformed to fulfil the requirements of parametric statistics (Sokal and Rohlf, 1995). The probability of occurrence of young cacti under open and sheltered microhabitats was compared by likelihood-ratio G-tests of goodness of fit, using the relative availability of the two microhabitats in the field as expected values under a random recruitment process (Sokal and Rohlf, 1995). To calculate the probability of recruitment of each cactus species under particular shrub species, likelihood-ratio G-tests were performed for each cactus – shrub association, using the number of young cacti under the focal shrub species and under the remaining shrubs as observed entries.

2.3. Abiotic conditions of microhabitats

At each microhabitat, I recorded the temperature and relative humidiy using data-logger sensors (HOBO Pro v2 / U23-002; one sensor for SM and two sensors for OM). Data-logger sensors were placed above ground level (i) under the shrub canopy (SM) or (ii) on bare soil completely free of any daytime shadow (OM). The variables were recorded every 30 min during five consecutive days during the seed dispersal season of cacti (December 2009), the period in which the conditions are more stressful due to higher temperatures and reduced water availability for plants.

In addition to broad microhabitat characterization, I sampled the soil under the canopy of *B. ambrosioides*, *B. incisifolia*, *F. thurifera*, *H. stenophyllum*, *P. chilensis* and bare soil to establish the hydric content by gravimetry. To this end, I weighed soil samples *in situ* (0.1 g precision) and stored them in seal plastic bags. At the laboratory, soil samples were dried at 70° C during 72 h and weighed again. Additionally, I carried out a basic analysis of chemical and physical characteristics of soil samples following standard procedures (INIA, 2006) to characterize pH and electric conductivity and to quantify total nitrogen, phosphorus, Na^+, K^+, Mg^{2+} and Ca^{2+}.

The abiotic conditions (T° and relative humidity) of microhabitats were compared using Kruskal-Wallis tests. The hydric content in summer and winter, and soil composition (each soil parameter separately) were compared using Kruskal-Wallis with *a posteriori* multiple comparisons of mean ranks for all groups to detect specific differences among microhabitats and among soil physical and chemical characteristics, respectively (Sokal and Rohlf, 1995).

2.4. Growth and survivorship assessment of young cacti

I tagged and geo-referenced 131 out of the 171 young cacti mentioned above (section 2.2) to follow and estimate growth and survivorship in a two-year period (from May 2009 to June 2011). To this end, I quantified the height and survivorship of plants in December 2009, May 2010, January 2011, and June 2011. Additionally, I recorded the potential cause of cactus mortality such as desiccation, herbivory, parasitism or fungal infection.

Growth was compared between species and microhabitats using a factorial ANOVA. Data were log-transformed to fulfil the requirements of parametric statistics (Sokal and

Rohlf, 1995). The mortality for each cactus species was compared using Fisher's exact test

(Sokal and Rohlf, 1995).

3.1. Recruitment and height of young cacti

I detected 110 and 61 young cacti of *E. chiloensis* and *E. acida*, respectively. The frequency of young cacti was lower near to the putative parent (0.0-0.5 m; Fig. 2), where parental shadow could have a stronger conspecific nurse effect. The two cactus species did not differ in the distance of recruitment (mean ± SE; *E. chiloensis*: 3.23 m ± 0.18 and *E. acida*: 4.33 m ± 0.47; $F_{1,109} = 1.52$, $P = 0.219$).
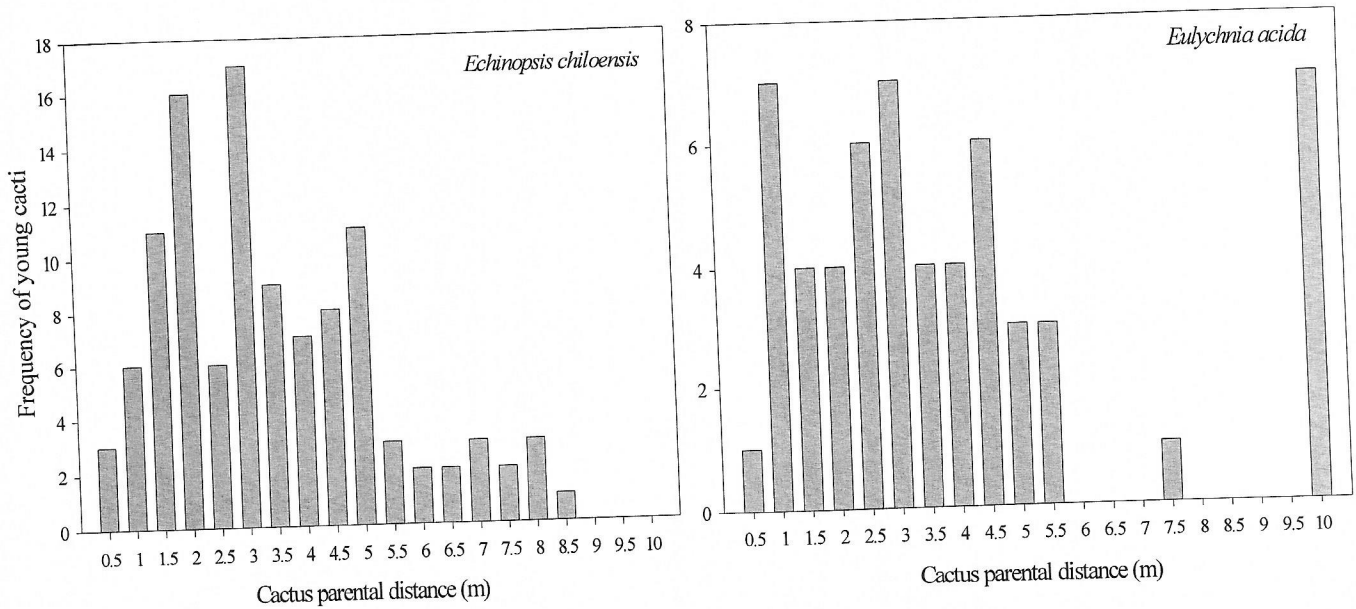

Fig. 2. Frequency of young cacti of *E. chiloensis* and *E. acida* according to the distance from their putative parental cacti (m). Each bar represents a range of 50 cm distance.

The height of the sampled individuals (Fig. 3) differed between microhabitats but not between species (mean ± SE (cm); *E. chiloensis*: SM = 0.15 ± 0.009, OM = 0.15 ± 0.009; *E. acida*: SM = 0.13 ± 0.013, OM = 0.19 ± 0.015, species: $F_{1,167} = 0.07$, $P = 0.786$; microhabitat: $F_{1,167} = 8.77$, $P = 0.003$; species × microhabitat: $F_{1,167} = 6.46$, $P = 0.011$). *A posteriori* HDS Tukey's tests indicate that the height of *E. acida* but not *E. chiloensis* differed between microhabitats ($P = 0.004$).
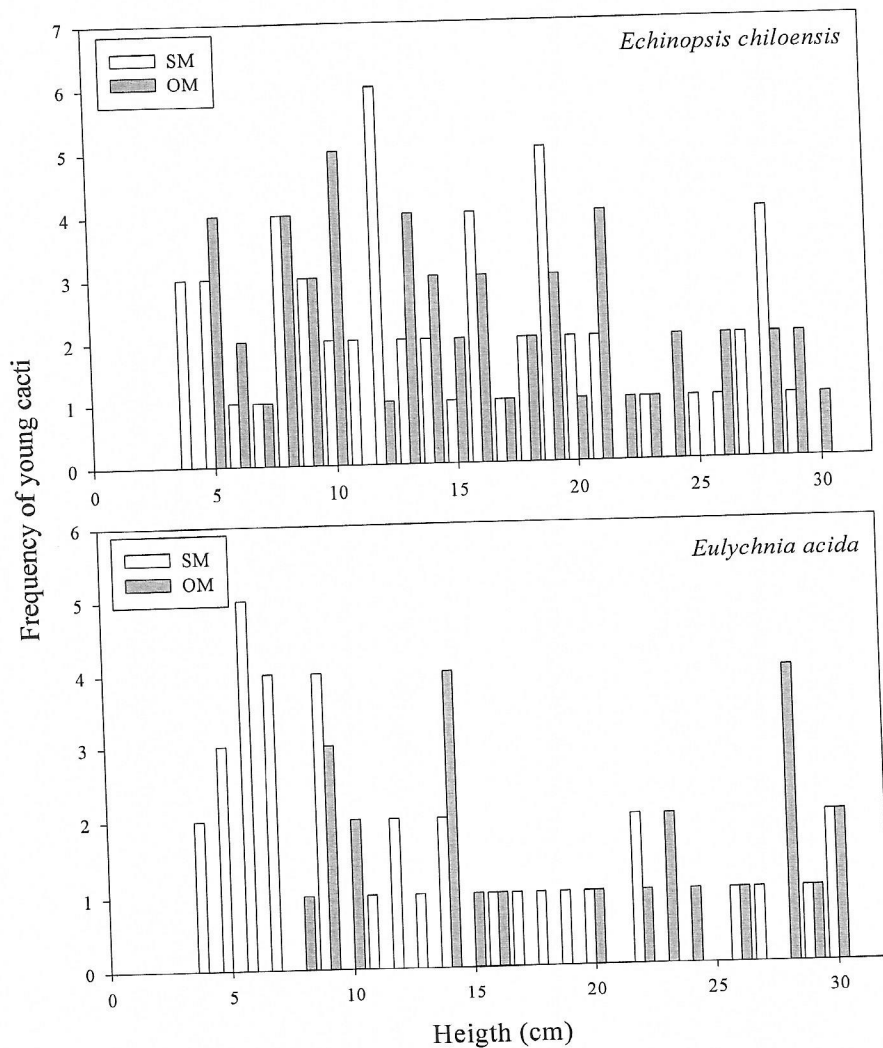

Fig. 3. Frequency of height (cm) of young cacti of *E. chiloensis* and *E. acida* in both sheltered (SM) and open (OM) microhabitats.

The relative availability of open and sheltered microhabitats in the study site was similar (53% and 47%, respectively). About 51% of the sampled young cacti of *E. chiloensis* occurred under shrubs. When compared with the expected value according to the relative availability of shrubs in the site, this percentage was not significant (G_{adj}= 2.951, p = 0.086). Regarding *E. acida*, a higher number of young cacti occurred under shrubs (60%), which differed statistically from the probability of cactus occurrence expected under a random process (G_{adj} = 6.393, P = 0.012).

In general, most cactus recruitment occurred under the shrub *F. thurifera* (81.3% for *E. chiloensis*, 76% for *E. acida*), in part due to the high relative abundance of this species in the field (74.9%), followed by *B. incisifolia* (10.2% for *E. chiloensis*, 8% for *E. acida*), *B. ambrosioides* (1.7% for *E. chiloensis*, 16% for *E. acida*), *P. chilensis* (5.1% for *E. chiloensis*, 0% for *E. acida*), and *H. stenophyllum* (1.7% for *E. chiloensis*, 0% for *E. acida*) (Table 1). However, some particular shrub species influenced the chance of recruitment beyond their relative availability. For example, young *E. chiloensis* were associated with *F. thurifera* more frequently than expected by chance (Fig. 4) suggesting that this shrub acts as nurse plant for *E. chiloensis*. Similarly, although the percentage of occurrence of young *E. acida* under *B. ambrosioides* was relatively low, this species occurred in a higher proportion than expected by chance. On the other hand, the percentage of occurrence of young *E. chiloensis* under *B. incisifolia* was lower than expected by chance, suggesting an inhibit process (Fig. 4).

Shurb species	Relative abundance
Flourensia thurifera	74.9
Bridgesia incisifolia	20.4
Porliera chilensis	1.9
Echinopsis chiloensis	1.8
Bahia ambrosioides	0.6
Eulychnia acida	0.2
Helliotropium stenophillum	0.0

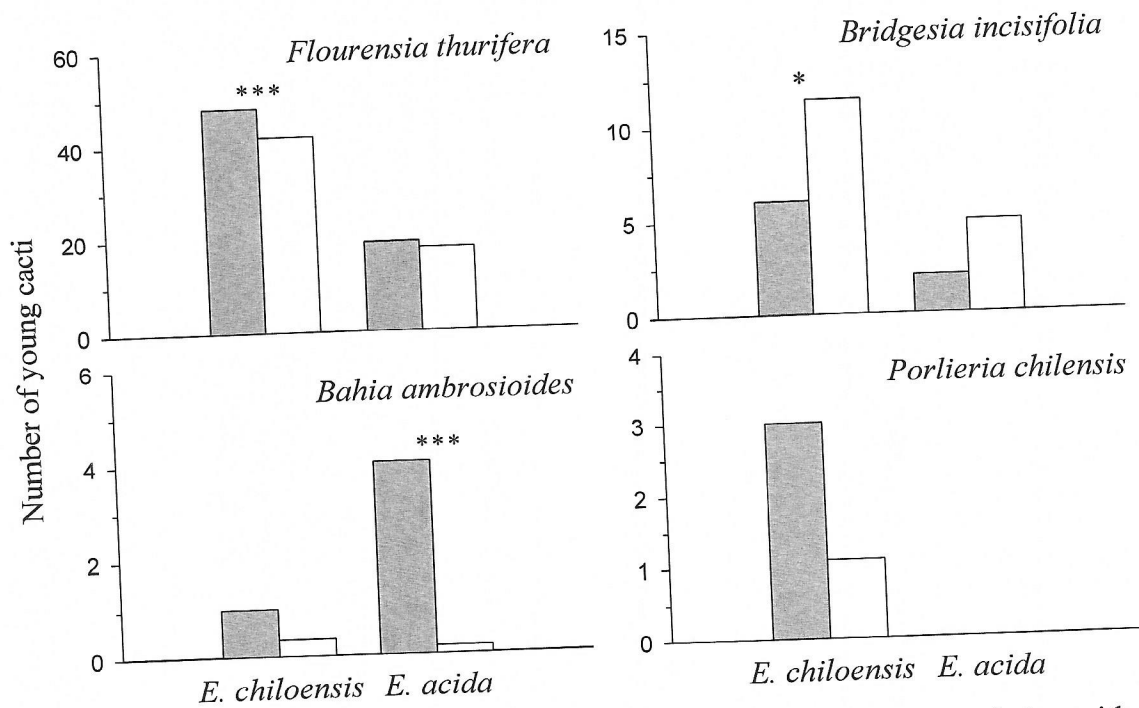Table 1. Relative abundance of shrub species in the study site including both cactus species.

Fig. 4. Number of young cacti of *E. chiloensis* and *E. acida* found in association with shrub species. Dark bars represent the observed number of young cacti under shrubs. White bars indicate the expected number of young cacti under shrubs based on the relative abundance of the shrub species in the field. *** $P < 0.001$, * $P < 0.05$

3.2. Abiotic conditions of microhabitats

The two microhabitats differed in their abiotic conditions. In general, lower temperatures were recorded under shrubs (SM) than in the open microhabitat (OM). The mean temperature under shrubs was 2° C lower than on bare soil, and the maximum temperature reached up to 44° C under shrubs and 47° C on bare soil in the summer season (Table 2).

Abiotic variable	SM	OM	H	P
Min T (°C)	20.11 ± 0.51 (5)	20.35 ± 0.62 (10)	0.06	0.806
Max T (°C)	44.61 ± 0.61 (5)	47.36 ± 0.60 (10)	6.01	**0.014**
Mean T (°C)	29.56 ± 0.53 (5)	31.23 ± 0.42 (10)	4.33	**0.037**
RH (%)	27.25 ± 1.58 (5)	28.71 ± 1.25 (10)	0.24	0.624

Table 2. Abiotic conditions (mean ± SE) in sheltered (SM) and open (OM) microhabitats. T: temperature; RH: relative humidity. Results from Kruskal-Wallis Test (H, P). Figures in parentheses indicate sample size (number of days).

The hydric content of the soil under shrubs was greater and differed significantly from open microhabitats in the summer season ($H_{5,30}$ = 11.45, P = 0.043). This effect occurred due to the significant difference between *B. incisifolia* and bare soil (P = 0.038), where the water content was higher under the shrub. Similarly, significant differences were detected in winter ($H_{4,25}$ = 14.27, P = 0.006), with lower water content in bare soil than under shrubs. These differences were given between *P. chilensis* and bare soil (P = 0.030) and *P. chilensis* and *B. ambrosioides* (P = 0.030), where *P. chilensis* showed the highest water content (Fig. 5).
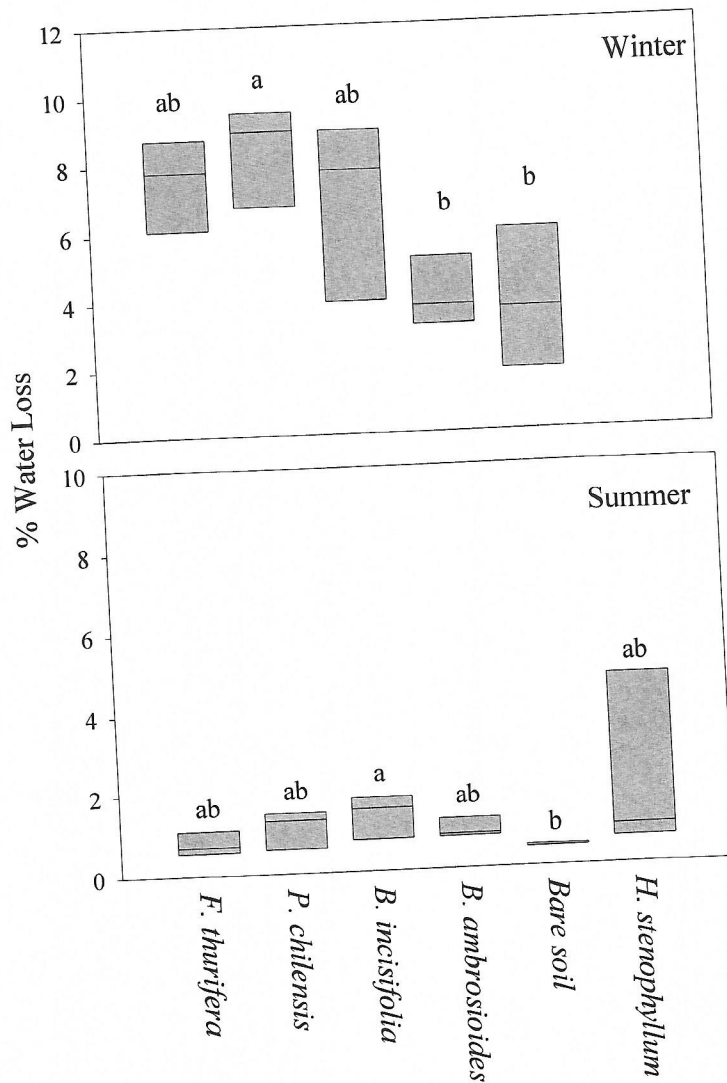
Fig. 5. Hydric content (% water loss) of soil samples under shrubs and bare soil (median and inter-quartile range) in summer and winter ($n = 5$). Different letters show significant differences between microhabitats.

Soil physical and chemical characteristics are shown in Appendix 1. Overall, soil samples differed only in phosphorus, total nitrogen, and calcium depending on species and microhabitats. Phosphorus content differed among *F. thurifera* (the nurse plant of *E. chiloensis*), bare soil and other plants ($H_{2,18} = 6.88$, $P = 0.032$). *Flourensia thurifera*

15

differed from bare soil (*post hoc* test, $P = 0.05$). Total nitrogen differed among microhabitats ($H_{2,18} = 6.37$, $P = 0.041$). Unlike phosphorus, differences were detected in the comparison bare soil and non-nurse plants but no effect was detected for *F. thurifera*. Regarding *B. ambrosioides* (the nurse plant of *E. acida*), only phosphorus and calcium differed among microhabitats ($H_{2,18} = 6.75$, $P = 0.034$ and $H_{2,18} = 6.37$, $P = 0.041$, respectively). *A posteriori* comparisons revealed that soil under *B. ambrosioides* did not show different phosphorus content than the other microhabitats. However, calcium availability was higher than the other non-nurse plants combined (*post hoc* test, $P = 0.04$).

3.3. Growth and survivorship assessment of young cacti

I tagged 94 and 37 young cacti of *E. chiloensis* and *E. acida*, respectively. In the two year period, *E. chiloensis* and *E. acida* grew 5.98 ± 0.45 and 5.71 ± 0.65 cm, respectively. No significant effect was detected between species or microhabitats (mean $\pm$ SE (cm); *E. chiloensis*: SM = 5.84 ± 0.54, OM = 6.19 ± 0.66; *E. acida*: SM = 5.56 ± 0.65, OM = 6.11 ± 1.74, species: $F_{1,121} = 0.36$, $P = 0.547$; microhabitat: $F_{1,121} = 0.01$, $P = 0.923$; species × microhabitat: $F_{1,121} = 0.08$, $P = 0,778$; Fig. 6).
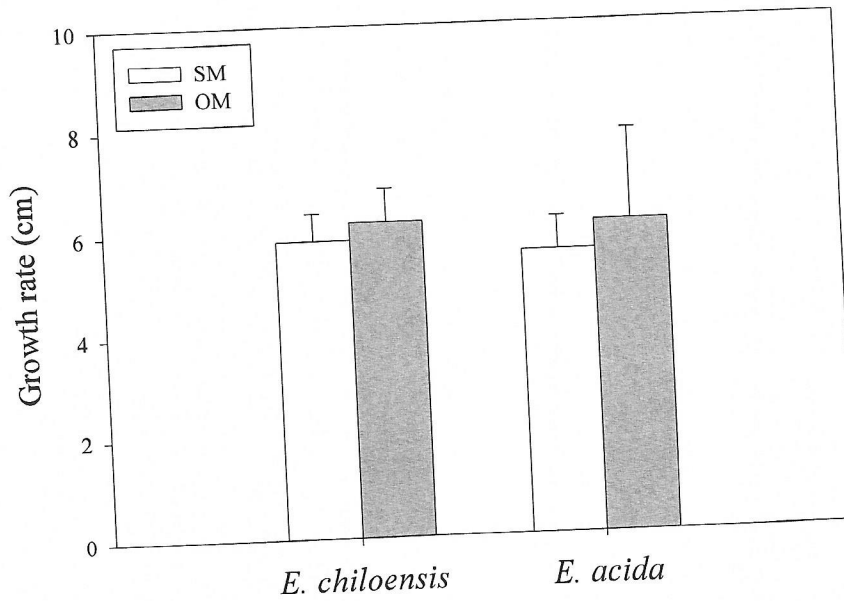
Fig. 6. Growth of *E. chiloensis* and *E. acida* in the two-year period (mean ± SE). Dark bars represent sheltered (SM) and white bars open (OM) microhabitats. Bars show mean and one standard error.

Overall, five young cacti (two *E. chiloensis* and three *E. acida*) died seemingly due to herbivory by rodents. Mortality reached to 2.1 and 8.1% for *E. chiloensis* and *E. acida*, respectively, in the two-year period. Non-significant differences were detected in mortality between microhabitats for *E. chiloensis* ($P = 0.63$) and *E. acida* ($P = 0.62$).

DISCUSSION

In this study I examined the rol of shrubs on cactus seedling recruitment and the association of shrub plants with young cactus seeding occurrence. Several studies have shown the importance of favourable microhabitats for germination success and seedling establishment, and exhibit the causes of nurse-seedling relationships (Turner et al., 1966; Franco and Nobel, 1989; Rojas-Aréchiga and Vásquez-Yanes, 2000; Flores and Jurado, 2003). Data from this study suggest that bare soils reduce the chance of successful cactus establishment, probably due to the higher mean and maximum temperatures associated to this microhabitat. Our results from standard soil analyses show that phosphorus differed between microhabitats. Higher concentration of phosphorus under shrubs compared with bare soil suggests that may be an important element for shrub (Nobel, 1989) and probably cactus development. However, soil physical and chemical characteristics do not seem to play an important role in the recruitment of both cactus species, as it has been reported in other studies (Arriaga, 1993). Nevertheless, soil chemistry may be involved in the form of specific allelopathic compounds that mediate cactus recruitment under *F. thurifera* in semiarid Chile. *Flourensia thurifera* is a native large drought-deciduous spineless shrub with leaves that stay on the branches even in the dry season. This species provides good quality shade due to its architecture and highly dense canopy. Interestingly, a previous study reported important allelopathic effects of *F. thurifera* on forbs, grasses, and shrubs, hence reducing local plant species richness in Chilean semiarid ecosystems (Fuentes et al., 1987). Whether *F. thurifera* protects *E. chiloensis* from direct sources of mortality (e.g.,

dessication, herbivory; Faini et al., 1997) and/or reduces the effects of competition with other plants including *E. acida*, need to be assessed in future studies (Fuentes et al., 1987).

The observation that the young cacti of *E. chiloensis* and *E. acida* occurred under *F. thurifera* and *B. ambrosioides*, respectively, more frequently than expected by chance suggests that some shrub species may play an important role in cactus recruitment in this system. Although for *E. chiloensis* the global effect of sheltered microhabitat was not significant, the recruitment under *F. thurifera* (nurse plant of *E. chiloensis*) was clearly higher than expected by chance compared with bare soil and other non-nurse shrubs (G_{adj}= 14.68, $P < 0.001$). This finding may be consistent with previous studies documenting a key role of nurse plants for seed germination and seedling establishment in cacti (Valiente-Banuet and Ezcurra, 1991; Godínez-Álvarez et al., 1999; Larrea-Alcázar and Soriano, 2008; Landero and Valiente-Banuet, 2010). Valiente-Banuet and colleagues (1991a,b) showed the nurse effect for five cactus species under perennial shrubs, and showed a positive association of young cacti of *Neobuxbaumia tetetzo* and *Mimosa luisana*, in the Zapotitlán Las Salinas' Valley. In this study, the high proportion of young cacti of *E. chiloensis* and *E. acida* under *F. thurifera* and *B. ambrosioides*, respectively, indicates that these shrubs provide a suitable microhabitat for young cactus, suggesting a "nurse plant syndrome" by these shrub species (Turner et al., 1966). A hypothesis of selection for nurse-plant interaction suggests that shrubs act as "seed trapping" (Flores and Jurado, 2003), that is, nurse-plant interactions may result from seed movement by wind or water across the soil surface that tends to accumulate seeds under established plants (El-Bana et al., 2002), or through seed disperser species like birds perching on branches, which would increase seed

accumulation under shrubs (McAuliffe, 1988). Nevertheless, the ability of nurse plants to capture seeds under their canopies should be experimentally tested under field conditions.

The fact that microhabitat had no effect on the growth of cacti suggests that young cactus growth might be limited by the nurse plant, for example, by competition for water with the nurse plant. Other experimental studies have shown that the water status and above-ground productivity of plants improve when the neighbors are removed (Franco and Nobel, 1989). In the same vein, this might explain the fact that *E. chiloensis* young cacti recruit less than expected by chance under *B. incisifolia* suggesting stronger resource competition. Some plants are better nurse plants than others, indicating species-specific relationships (Callaway and D' Antonio, 1991; Callaway, 1998). In this study I show that there is a species-specific effect of nurse plants given by the relationship *E. chiloensis - F. thurifera* and *E. acida - B. ambrosioides*.

Interestingly, I found significant differences between sheltered and open microhabitat in the initial height of young cacti of *E. acida*, but not in *E. chiloensis*. This suggests that microhabitat is relevant for the former species in terms of growth. The lowest height found in sheltered microhabitat could be due to competition for water with shrub species, as explained above, which would reduce the growth of young cacti under shrubs. Other not mutually exclusive explanation could be that small young cacti in open microhabitat are subjected to higher herbivory pressure, which would result in a higher frequency of taller young cacti - those which escape from herbivory - in open than sheltered microhabitat. Notwithstanding, these hypotheses need to be tested.

The relative abundance of adult cacti (> 1m height) of *E. chiloensis* and *E. acida* in the study area is close to 4:1, respectively (three slopes sampled, 641 *E. chiloensis* and 154

20

E. acida). This proportion differs from the proportion of young cacti for the two species in the same area (3.3 hectares), 2:1 (110 *E. chiloensis* and 61 *E. acida*) ($\chi^2_1 = 21.61$, $P < 0.0001$). This difference suggests that the survival in the transition from young cacti to adult is higher in *E. chiloensis* than *E. acida*. At least, three not mutually exclusive hypotheses related to biological interactions may be suggested to explain this result. Firstly, the low number of adult *E. acida* compared to *E. chiloensis* may be due to a bottle neck event in the past assuming that the former is a more sensitive species to stressful abiotic conditions during the transition from young cacti to adult. Secondly, *E. acida* may receive a higher herbivory in the transition from young cacti to adult. Partial support to this idea comes from the higher mortality recorded for *E. acida* seedlings in a period of two years, but more herbivory events are required to formally test this hypothesis. Thirdly, seedling growth of desert species can be significantly reduced by neighboring adult plants (Gurevitch 1986), therefore, it is likely that young cacti of *E. acida* perform suboptimally when competing for suitable microhabitats.

Cactaceae is a group of plants characterized by high levels of endemism, which in Chile reaches a 80% (Ortega-Baes and Godínez-Álvarez, 2006); therefore, is necessary to increase the knowledge of this group on frugivory and seed dispersal, seed bank dynamics, recruitment, and importance of nurse plants in the establishment and growth of seedling of columnar cacti in Chile. In this study, I quantified the occurrence, growth and survivorship of two cactus species. At the same time, I described the potential role of nurse plants and their importance during the earliest life-cycle stages of the two most abundant columnar cacti. It is not only important to assess the distribution and abundance of cactus species but

also the factors affecting these parameters to develop and establish appropriate regulations and management plans in the near future.

REFERENCES

Arriaga, L., Maya, Y., Diaz, S., Cancino, J., 1993. Association between cacti and nurse perennials in a heterogeneous tropical dry forest in northwestern Mexico. J. Veg. Sci. 4, 349–356.

Callaway, R.M. 1998. Competition and facilitation on elevation gradients in subalpine forest of the northern Rocky Mountains, USA. Oikos. 82, 561–573.

Callaway, R.M., D'Antonio, C.M. 1991. Shrub facilitation of coast live oak establishment in central California. Madrono 38,158–169.

Carrillo-García, A., Bashan, Y., Bethlenfalvay, G.J., 2000. Resource-island soils and the survival of the giant cactus, cardon, of Baja California Sur. Plant Soil. 218, 207–214.

di Castri, F., Hajek, E.R., 1976. Bioclimatología de Chile. Ediciones de la Universidad Católica de Chile, Santiago.

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. J. Arid Environ. 65, 46–61.

El-Bana, M.I., Nijs, I., Kockelbergh, F. 2002. Microenvironmental and vegetational heterogeneity induced by phytogenic nebkhas in an arid coastal ecosystem. Plant Soil. 247, 283–293.

Faini, F., Labbe, C., Salgado, I., Coll, J. 1997. Chemistry, toxicity and antifeedant of the resin of *Flourensia thurifera*. Biochem. Syst. Ecol. 25, 189–193.

Flores, J., Jurado, E., 2003. Are nurse-protégé interactions more common among plants from arid environments? J. Veg. Sci. 14, 911–916.

Franco, A.C., Nobel, P.S., 1989. Effect of nurse plant on the microhabitat and growth of cacti. J. Ecol. 77, 870–886.

Fuentes, E.R., Espinoza, G.A., Gajardo, G., 1987. Allelopathic effects of the Chilean matorral shrub *Flourensia thurifera*. Rev. Chil. Hist. Nat. 60, 57–62.

Godínez-Álvarez, H., Valiente-Banuet, A., Valiente Banuet, L., 1999. Biotic interactions and population dynamics of the long-lived columnar cactus *Neobuxbaumia tetetzo* in the Tehuacán Valley, Mexico. Can. J. Bot. 77, 203–208.

Godínez-Álvarez, H., Valverde, T., Ortega-Baes, P., 2003. Demographic trends in the Cactaceae. Bot. Rev. 69, 173–203.

Gurevitch, J., 1986. Competition and the local distribution of the grass *Stipa neomexicana*. Ecology. 67, 46–57.

Hoffmann, A., 1989. Cactáceas en la flora silvestre de Chile. Ediciones Fundación Claudio Gay, Santiago.

Hoffmann, A.E., Walter, H.E., 2004. Cactáceas en la flora Silvestre de Chile. Ediciones Fundación Claudio Gay, Santiago.

Hunt, D., 2006. The new cactus lexicon. Dh, Milborne Port.

Hutto, R.L., McAuliffe, J.R., Hogan, L., 1986. Distributional associates of the saguaro (*Carnegiea gigantea*). Southwest. Nat. 31, 469–476.

INIA, 2006. Métodos de Análisis de Suelo. Serie La Platina, 16.

Landero, J.P.C., Valiente-Banuet, A., 2010. Species-specificity of nurse plants for the establishment, suvivorship, and growth of a columnar cactus. Am. J. Bot. 97, 1289–1295.

Larrea-Alcázar, D.M., Soriano, P.J., 2008. Columnar cacti-shrub relationships in an Andean semiarid valley in western Venezuela. Plant Ecol. 196, 153–161.

Luebert, F., Pliscoff, P., 2006. Sinopsis Bioclimática y Vegetacional de Chile. Editorial Universitaria, Santiago, Chile.

Mandujano, M.C., Montaña C., Mendez, I., Golubov, J. 1998. The relative contributions of sexual reproduction and clonal propagation in Opuntia rastrera from two habitats in the Chihuahuan desert. J. Ecol. 86, 911–921.

Martínez del Río, C., Hourdequin, M., Silva, A., Medel, R., 1995. The influence of cactus size and previous infection on bird deposition of mistletoe seeds. Aust. J. Ecol. 20, 571–576.

McAuliffe, J.R. 1988. Markovian dynamics of simple and complex desert plant communities. Am. Nat. 131, 459–490.

Medel, R., 2000. Assessment of parasite-mediated selection in a host-parasite system in plants. Ecology 81, 1554–1564.

Medel, R., Vergara, E., Silva, A., Kalin-Arroyo, M., 2004. Effects of vector behavior and host resistance on mistletoe aggregation. Ecology 85, 120–126.

Medel, R., Botto-Mahan, C., Smith-Ramirez, C., Mendez, M.A., Ossa, C.G., Caputo, L., Gonzáles, W.L., 2002. Historia natural cuantitativa de una relación parásito-hospedero: el sistema *Tristerix*-cactáceas en Chile semiárido. Rev. Chil. Hist. Nat. 75, 127–140.

Medel, R., Méndez, M., Ossa, C.G., Botto-Mahan, C., 2010. Arms race coevolution: the local and geographical structure of a host-parasite interaction. Evolution, Education & Outreach 3, 26–31.

Muro-Pérez, G., Jurado, E., Flores, J., Sánchez-Salas, J., García-Pérez, J., Estrada, E. 2011. Positive effects of native shrubs on three specially protected cacti species in Durango, México. Plant Spec. Biol. 27, 53–58.

Nobel, P.S., 1980. Morphology, nurse plants, and minimum apical temperatures for young Carnegiea gigantean. Bot. Gaz. 141, 188–191.

Nobel, P.S., 1989. Temperature, water availability, and nutrients levels at various soil depths. Consequences for shallow –rooted desert succulents, including nurse plant effects. Am. J. Bot. 76, 1486–1492.

Ortega-Baes, P., Godínez-Álvarez, H., 2006. Global diversity and conservation priorities in the Cactaceae. Biodivers. Conserv. 15, 817–827.

Rojas-Aréchiga, M, Vázquez-Yanes, C., 2000. Cactus seed germination: a review. J. Arid Environ. 44, 85–104.

Sokal, R.R., Rohlf, F.J., 1995. Biometry. The principles and practice of statistics in biological research. WH Freeman & Company, New York.

Suzán-Azpiri, H., Sosa, V.J., 2006. Comparative performance of the giant cardon cactus (*Pachycereus pringlei*) seedlings under two leguminous nurse plant species. J. Arid Environ. 65, 351–362.

Turner, R. M., Alcorn, S.M., Olin, G., Booth, J.A., 1966. The influence of shade, soil, and water on saguaro seedling establishment. Bot. Gaz. 127, 95–102.

Valiente-Banuet, A., Ezcurra, E., 1991. Shade as a cause of the association between the cactus *Neobuxbaumia tetetzo* and the nurse plant *Mimosa luisana* in the Tehuacán Valley, Mexico. J. Ecol. 79, 961–971.

Valiente-Banuet, A., Vite, F., Zavala-Hurtado, J.A., 1991a. Interaction beween the cactus *Neobuxbaumia tetetzo* and the nurse shrub *Mimosa luisana*. J. Veg. Sci. 2, 11–14.

Valiente-Banuet, A., Bolongaro-Crevenna, A., Briones, O., Ezcurra, E., Rosas, M., Núñez, H., Barnard, G., Vásquez, E., 1991b. Spatial relationships between cacti and nurse shrubs in a semi-arid environments in central Mexico. J. Veg. Sci. 2, 15–20.

Valiente-Banuet, A., Arizmendi, M., Rojas-Martínez, A., Casas, A., Godínez-Álvarez, H., Silva, C., Dávila-Aranda, P., 2002. Biotic interactions and population dynamics of columnar cacti. In: Fleming, T.H., Valiente-Banuet, A. (Eds.), Columnar cacti and their mutualists: evolution, ecology, and conservation. University of Arizona Press, Tucson, pp. 225–240.

APPENDIX 1

Variable	Microhabitat					
	F. thurifera	B. ambrosioides	P. chilensis	B. incisifolia	H. stenophyllum	Bare soil
CE (µS/cm)	113.00 ± 22.81	156.66 ± 32.06	167.67 ± 99.68	46.67 ± 13.17	230.33 ± 125.49	59.33 ± 28.81
pH	7.08 ± 0.07	7.03 ± 0.14	6.98 ± 0.29	6.52 ± 0.13	7.16 ± 0.14	7.28 ± 0.41
Phosphorus	37.92 ± 3.19	37.46 ± 3.72	49.46 ± 17.08	23.86 ± 1.83	49.18 ± 11.48	18.44 ± 3.13
Total nitrogen	577.87 ± 62.61	833.77 ± 306.37	1958.33 ± 449.00	777.96 ± 295.29	1110.37 ± 129.34	263.60 ± 116.35
Na^+	52.03 ± 13.24	66.23 ± 6.03	108.01 ± 69.16	20.89 ± 5.64	167.46 ± 115.76	41.27 ± 5.69
K^+	122.65 ± 23.38	187.76 ± 70.66	46.09 ± 33.96	9.66 ± 2.41	44.74 ± 27.04	37.54 ± 12.88
Mg^{2+}	19.74 ± 3.98	27.93 ± 2.12	75.21 ± 41.48	14.99 ± 6.29	45.17 ± 13.01	13.68 ± 4.83
Ca^{2+}	50.92 ± 9.82	27.93 ± 2.12	16.85 ± 7.81	6.91 ± 2.01	9.76 ± 2.75	29.19 ± 14.16

Table 2. Parameters of physical and chemical composition of soil samples (mean $\pm$ 1 SE, N = 3) analyzed for each microhabitat. CE: electric conductivity.