

# SPECIES-SPECIFICITY OF NURSE PLANTS FOR THE ESTABLISHMENT, SURVIVORSHIP, AND GROWTH OF A COLUMNAR CACTUS<sup>1</sup>

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- **Premise of the study:** Seedling establishment and early survivorship are crucial steps for the regeneration of plant populations because both have long-lasting effects on plant population dynamics. For species recruiting through facilitation, species-specific facilitative effects might affect early fitness, an overlooked aspect in studies of facilitation considering groups of nurse species.
- **Methods:** We experimentally evaluated the roles of 10 nurse species and open space on the early performance of the columnar cactus *Neobuxbaumia mezcalaensis*. We measured establishment, survivorship, and growth of individuals over 3 years. Moreover, to study an extended period of the ontogeny of the interaction between this cactus and its nurse plants, we also monitored survivorship and growth rates of individuals between 3 to 12 cm tall during a 3-year period.
- **Key results:** *Neobuxbaumia mezcalaensis* performance varied significantly among nurse species, and only six yielded positive effects on early fitness. Densely canopied plants were the best nurses for this cactus. However, even among densely canopied species, some produced negative effects on the early fitness of *N. mezcalaensis*, indicating that similar nurse plants may elicit either facilitative or interference effects on beneficiary species.
- **Conclusions:** Our results emphasize the importance of species-specific facilitative interactions in the crucial early stages in the life cycle of *N. mezcalaensis* and how different nurse species modify the effect of seed-rain and contribute significantly to the population dynamics of the species.

**Key words:** Cactaceae; competition; Mexico; *Neobuxbaumia mezcalaensis*; nurse plants; seedling establishment; species-specific facilitative interactions; Tehuacán-Cuicatlán Valley.

Facilitation occurs when the presence of one plant enhances the growth, survival, and reproduction of a neighbor (Callaway, 2007). The main facilitative mechanisms provided by nurse plants are the amelioration of the microclimate beneath their canopies (Valiente-Banuet and Ezcurra, 1991; Callaway, 1992; Gómez-Aparicio et al., 2004), protection from herbivores (Callaway et al., 2000; Obeso and Fernández-Calvo, 2003; García and Obeso, 2003; Baraza et al., 2006), the improvement of physical, chemical, and biological soil properties (Rebollo et al., 2002; Carrillo-García et al., 1999; Puerta-Piñero et al., 2006). However, not all apparently similar nurse plant species play the same facilitative role (Callaway, 1998). Thus, from a group of co-occurring species, some plants are better facilitators than others, indicating species-specific facilitative relationships (Callaway and D'Antonio, 1991; Callaway, 1998). According to Callaway (1998, 2007), the occurrence of species-specific positive interactions suggests tighter interdependence in plant communities, considering that the absence of a given

nurse species and thus regeneration by a dependent beneficiary species may result in the absence of some species in the community.

Seedling establishment and early survivorship are crucial steps in the regeneration of plant populations; the highest mortality rates commonly occur after the seeds are dispersed into different microenvironments (Schupp, 1995; Ibañez and Schupp, 2002; Traveset et al., 2003; Castro et al., 2004). Consequently, what occurs during these steps greatly determines the dynamics and spatial patterns of recruitment, which in turn has long-lasting effects on plant populations and communities (Harper, 1977; Goldberg and Werner, 1983; Clark et al., 1999). These steps are greatly affected by abiotic factors (i.e., the occurrence of heavy rainfall events), along with positive and negative interactions, affect seedling emergence, survival, and growth. For example, in long-lived species such as the columnar saguaro cactus (*Carnegiea gigantea*), survivorship curves of type III have been reported, characterized by a high mortality during the first 7 years, after which the number of remaining individuals is maintained unless sporadic and normally unpredictable dry and freezing events occur (Steenbergh and Lowe, 1969, 1983; Pierson and Turner, 1998). Similarly, columnar cacti such as *Neobuxbaumia tetetzo* (Valiente-Banuet and Ezcurra, 1991; Godínez-Alvarez et al., 1999, 2002) and *Neobuxbaumia macrocephala* (Godínez-Alvarez and Valiente-Banuet, 2004), which inhabit tropical areas that do not undergo freezing events, have their highest mortality rates during the first 3 years; after this period, few changes in the population are reported. For many cactus species, seedling establishment is completely dependent on heavy rainfall events occurring over several consecutive

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days (Steenbergh and Lowe, 1977) and occurs successfully only through facilitation (Valiente-Banuet and Ezcurra, 1991). A plethora of studies have reported both of these factors and lower frequencies of early life stages, with more cactus associated under some nurse species than others (Steenbergh and Lowe, 1977; McAuliffe, 1986, 1988; Callaway and D'Antonio, 1991; Valiente-Banuet et al., 1991; Suzán et al., 1996), suggesting the existence of species-specific facilitative relationships (Turner et al., 1966; Callaway and D'Antonio, 1991; Callaway, 1998). However, the mechanisms of these positive and negative association patterns have rarely been analyzed from a species-specific perspective or through experimental manipulations. For example for some cacti, positive associations can be the result of an increase of survivorship of young facilitated individuals beneath certain species. This differential distribution of facilitated species with respect to nurse species may be the result of microclimatic modifications (Turner et al., 1966; Valiente-Banuet and Ezcurra, 1991; Drezner, 2006), the protection of seed and seedlings from browsing animals (Baraza et al., 2006), the effect of other organisms (i.e., mycorrhizae; Carrillo-García et al., 2000a; Puerta-Piñero et al., 2006), the formation of fertility islands (Franco and Nobel, 1989), as well as interference interactions (Muller, 1953; Fonteyn and Mahall, 1981; De Viana et al., 2001; Cazón et al., 2002), and seed limitation (Turnbull et al., 2000). Consequently, the importance to determine to what extent plant–plant interactions provide or not regeneration niches for facilitated species is central to understand how plants respond to neighbors.

The dominant columnar cactus, *N. mezcalaensis* (Bravo) Backeberg, has been shown to recruit successfully only beneath the canopies of perennial plants, and its spatial patterns show a high degree of species-specificity correlations with nurse plants (Valiente-Banuet and Verdú, 2008).

In this study, we evaluated experimentally the roles of microhabitat modification by nurse plants for seed germination, seedling establishment, and survival as well as growth over three consecutive years. As an additional experiment, and to follow the ontogeny of the natural interaction between *N. mezcalaensis* and its nurse plants for a longer time, we monitored survivorship and growth rates of pre-established individuals between 3 and 12 cm tall that were associated with different nurse plant species.

We specifically asked: (1) Are these positive and negative association patterns produced by the species-specific effects of nurse species related to nurse architecture or are they due to seed availability, predation, or interference? (2) Is there any evidence that growth is affected by species-specific nurse plant effects?

## MATERIALS AND METHODS

**Species and study site**—*Neobuxbaumia mezcalaensis* is an unramified columnar cactus endemic to central Mexico growing to 12 m in height and 20–30 cm in diameter, with 13–20 ribs (Bravo-Hollis, 1991). Flowering and fruiting seasons are from April to June with an androdioecious reproductive system characterized by the presence of individuals with male or hermaphroditic flowers; nectar-feeding bats are the most important pollinators (Valiente-Banuet et al., 1997). Fruits are green and grow along the ribs on the side of the plant. They dehisce nocturnally, exposing a sugary whitish pulp, of a color and odor similar to flowers, thus corresponding to a bat dispersal syndrome (J. P. Castillo and A. Valiente-Banuet, unpublished data). This species only recruits successfully beneath the canopies of different perennial plants and the number of individuals growing beneath different nurse species varies greatly (Valiente-Banuet and Verdú, 2008).

*Neobuxbaumia mezcalaensis* is the dominant floristic component of a vegetation type known locally as a tetechera of *N. mezcalaensis* and *N. macrocephala*.

This tetechera is a columnar cacti forest located in the vicinity of San Juan Raya at 18°19'59.6"N, 97°38'4.7"W, and at 1770 m a.s.l. Mean annual temperature is 21°C, and annual precipitation is 380 mm (García, 1973). The most important shrub species in this community are *Lippia graveolens*, *Calliandra eriophylla*, *Mascagnia seleriana*, *Echinopteryx eglandulosa*, *Pseudosmodium multifolium*, *Acacia subangulata*, *A. constricta*, *Hechtia podantha*, *Cnidoscylus tehucanensis*, *Yucca periculosa*, and *Mimosa lacerata* (Valiente-Banuet et al., 2000).

**Seedling establishment, survivorship, and growth experiments**—Microhabitat effects on *N. mezcalaensis* establishment, survivorship, and growth after 3 years were evaluated experimentally. Experiments started at the end of the fruiting season of *N. mezcalaensis*, in the wet season between the months of June and July 2005. Seeds were randomly collected from ripe fruits obtained during 2005 from a total of 12 individuals. An establishment experiment was conducted with two factors: (1) predation, with two levels, in which *N. mezcalaensis* seeds were excluded and nonexcluded from predators, and (2) microhabitat, with 11 levels, i.e., open space, and the 10 most abundant perennial nurse plants found in the community. These species differed substantially in architecture. Included were species with dense canopies that produced homogeneous shade in the vertical projection of the crown such as *Cnidoscylus tehucanensis*, *Calliandra eriophylla*, *Lippia graveolens*, *Mimosa lacerata*, *Pseudosmodium multifolium*, and *Echinopteryx eglandulosa*. Species do not exceed 2 m in height. We included sparsely canopied shrubs consisting of two to three unramified stems rising from the ground with small leaves along the stems (*Acacia constricta*), plants taller than 2 m and having a small canopy characterized by a crown rosette of leaves no more than 30 cm long on the top of a single stem (*Yucca periculosa*), a single-stemmed plant without branches and leaves (*Neobuxbaumia mezcalaensis*), and a sparse grass less than 50 cm tall (*Bouteloua gracilis*).

Potential nurse species typically grow associated with other plant species, but in all cases the target benefactor species was the dominant species in the vegetation patch. Each experimental unit consisted of 50 seeds sown in a 15 × 10 cm plot and replicated five times. Experimental units excluded from predators were placed under a wire net cage (15 × 10 × 7 cm) nailed to the ground to prevent vertebrate predation (rodents and birds). Invertebrates, mostly ants, were excluded using the chlorine insecticide powder. Seeds were monitored daily until either seedlings emerged or were eaten. After seedling emergence, survivorship was monitored monthly for 3 years. At the end of the experiment, all individuals of *N. mezcalaensis* growing beneath the different nurse species were measured with a caliper to quantify the microhabitat effect on growth.

Seedling emergence was recorded 20 d after sowing, and survival data was recorded after 3 years in the different microhabitats and predator exclusion treatments. Data were analyzed by fitting generalized linear models (GLM) (McCullagh and Nelder, 1989) using a Poisson link distribution. The null hypothesis considered the same number of emerged seedlings under all treatments, and the same number of individuals surviving after 3 years, in all treatments. Differences in the height of the young individuals after 3 years growing in the different microhabitats were analyzed with a one-way ANOVA with a post hoc Tukey honestly significant difference (HSD) test. Analyses were performed with R Development Core Team (2008).

**Survival and growth rates of young pre-established individuals**—To study the ontogeny of the natural interaction between *N. mezcalaensis* and its nurse plants over a longer time period, we monitored survivorship and growth rates of 580 already established individuals between 3 and 12 cm in height (ca. 3- to 14-yr-old individuals; A. Valiente-Banuet, unpublished data) that had established naturally prior to this study and were associated with different nurse plant species. Individual plants were classified into three height categories: (1) ≤3 cm, (2) taller than 3 cm but ≤6 cm, and (3) taller than 6 cm but ≤12 cm. We placed a nail at the base of each individual, to ensure remeasurement of the height was carried out from the same reference point. Measurements were taken with a metal ruler from a metal nail in the ground, insuring accurate calibration among dates, to the top of the cactus. Seedling survival in each height category was measured 3 years after tagging. Growth was measured as the accumulated relative height growth (RHG) over 3 years, calculated as:  $(\ln H_2 - \ln H_1)/(t_2 - t_1)$ , where  $H_1$  and  $H_2$  are the measurements of the initial and final height and  $t_2 - t_1$  is the time between measurements.

Differences in survivorship were analyzed with a binomial logistic regression, with microhabitat and height category as independent variables and variable is a binary response variable of death or survival of individuals (Crawley, 2005). The null hypothesis was that survivorship of *N. mezcalaensis* individuals is not affected by microhabitat and plant height. Analyses were performed with R (R Development Core Team, 2008).

**Microhabitat effect on *N. mezcalaensis* performance**—To synthesize the microhabitat effect on *N. mezcalaensis* performance, we calculated the overall probability for a *N. mezcalaensis* seed to become a plant of 12 cm in height in each microhabitat. This overall probability was estimated as the product of the probability of seedling survival to 3 years after emergence, and the survival of pre-established *N. mezcalaensis* plants, in each height category and different microhabitat, 3 years after tagging.

## RESULTS

**Seed germination**—*Neobuxbaumia mezcalaensis* seeds started to germinate after a heavy rain that occurred on the same day we seeded, and the maximum number of established seedlings in all treatments was reached 20 d after seeding. The number of emerged seedlings under the different microhabitats differed significantly ( $\chi^2 = 193.44$ ,  $df = 10$ ,  $P < 0.0001$ ). The highest seedling emergence rates were recorded under densely canopied species *C. eriophylla*, *E. eglandulosa*, *L. graveolens*, *P. multifolium*, and *M. lacerata*, which had two to five times more germinated seeds than *A. constricta* with a large, sparse canopy and *Y. periculosa* with a short canopy (Table 1). Rates were more than 7 and 30 times greater than under *N. mezcalaensis* and open space. No germination was recorded under the sparse grass *B. gracilis* or under the densely canopied *C. tehuacanensis*.

Seedling emergence was almost four times higher when seeds were excluded from predators ( $\chi^2 = 193.44$ ,  $df = 1$ ,  $P < 0.0001$ ). Seed predation ranged between 78 and 100%, primarily by ants *Pogonomyrmex barbatus*, and by two bird species, *Zenaida asiatica* and *Columbina passerina*, all of which foraged on seeds when they were on the ground. However, no interaction between microhabitat and seed predation was detected ( $\chi^2 = 13.40$ ,  $df = 10$ ,  $P = 0.19$ ), indicating that no particular microhabitat protected against seed predators.

**Survival and growth 3 years after emergence**—Three years after emergence, the survival of *N. mezcalaensis* individuals from experimentally planted seeds varied significantly between microhabitats, ( $\chi^2 = 189.39$ ,  $df = 10$ ,  $P < 0.0001$ ). The highest

survival rates were observed beneath the densely canopied species *L. graveolens*, *P. multifolium* and *M. lacerata* with survival rates of 73.75%, 53.84% and 42.30%, respectively. For the other densely canopied species (*E. eglandulosa* and *C. eriophylla*) survival was very low, 8.8% and 4.8% of emerged seedlings, respectively. For the sparsely canopied species *A. constricta* survival was 7.7%. In contrast, for nurse species with short canopies (*N. mezcalaensis* and *Y. periculosa*), and for open space, there was no survival (Table 1).

The number of seedlings that survived for 3 years was significantly higher when herbivores were excluded ( $\chi^2 = 189.39$ ,  $df = 1$ ,  $P < 0.0001$ ); however, as before there was no significant interaction between microhabitat and seedling predation ( $\chi^2 = 1.59$ ,  $df = 10$ ,  $P = 1$ ), indicating that seedling predation was similar in all microhabitats.

The height of 3-year-old individuals growing beneath different nurse species differed significantly ( $F_{4,34} = 3.84$ ,  $P = 0.006$ ) ranging from 1.6 to 2.9 cm (Table 1). The tallest individuals were found beneath the densely canopied species *C. eriophylla*, *E. eglandulosa*, *P. multifolium* and *M. lacerata*, whereas the smallest plants were observed beneath densely canopied *L. graveolens* and the sparsely canopied *A. constricta*.

**Survival and growth of young pre-established individuals**—Survival of established *N. mezcalaensis* juveniles did not differ between microhabitats after the third year ( $\chi^2 = 13.36$ ,  $df = 8$ ,  $P = 0.16$ ), but survival did vary among height categories ( $\chi^2 = 13.82$ ,  $df = 2$ ,  $P = 0.002$ ; Fig. 1) with the highest survival for plants taller than 3 cm. Survival in the 1–3 cm category was 18%, the 3–6 cm category 27% ( $\chi^2 = 9.21$ ,  $df = 2$ ,  $P = 0.02$ ; Fig. 1), and the 6–12 cm category 32% ( $\chi^2 = 21.96$ ,  $df = 8$ ,  $P = 0.004$ ; Fig. 1). The interaction between microhabitat and height category was also significant, ( $\chi^2 = 350.87$ ,  $df = 506$ ,  $P = 0.006$ ) with the greatest survival under *A. constricta* (sparsely canopied); *C. eriophylla*, *E. eglandulosa*, *L. graveolens*, and *P. multifolium* (densely canopied); and *Y. periculosa* (short-canopied species) when plants were of a height greater than 3 cm. The lowest survival was under *N. mezcalaensis* (a short-canopied species) for the same height categories of seedlings.

Relative height growth after the third year varied significantly between microhabitats ( $F_{8,165} = 4.79$ ,  $P < 0.0001$ , Fig. 2), being significantly highest under *P. multifolium* (densely canopied species), with the rest of the other nurses species not differing among each other. No growth was detected beneath *N. mezcalaensis* (Fig. 2).

**Overall microhabitat effect on *N. mezcalaensis* survivorship**—Microhabitats had different effects on the probability of *N. mezcalaensis* seeds becoming 12 cm tall, ranging from highly positive for the densely canopied *M. lacerata* (1.3%), *L. graveolens* (0.9%), and *P. multifolium* (0.8%), to very low in the sparsely canopied *A. constricta*, and in the densely canopied *C. eriophylla* and *E. eglandulosa*. In contrast under the sparse grass *B. gracilis*, the densely canopied *C. tehuacanensis*, the short-canopied species *N. mezcalaensis* and *Y. periculosa* and in open space, none of the seedlings grew to 12 cm (Fig. 3).

## DISCUSSION

The main finding of this study is that of the 11 microhabitats evaluated, only six nurse species constitute safe sites for the establishment of *N. mezcalaensis* (sensu Harper, 1977). These

TABLE 1. Total number of emerged seedlings of *N. mezcalaensis*, survival after 3 years, and mean height 3 years after emergence seeded under the 11 microhabitats, excluded and nonexcluded from predators. A total of 250 seeds were sown for each treatment.

Microhabitat	Seedling emergence		Survival after 3yr		Height after 3 yr (cm)
	Excluded	Non excluded	Excluded	Non excluded	
<i>C. eriophylla</i>	123	55	6	0	2.9 ± 0.24 A
<i>E. eglandulosa</i>	112	16	9	0	2.5 ± 0.20 AB
<i>M. lacerata</i>	52	0	22	0	2.3 ± 0.13AB
<i>P. multifolium</i>	104	36	56	0	2.1 ± 0.12 AB
<i>L. graveolens</i>	80	27	59	0	1.9 ± 0.11 B
<i>A. constricta</i>	26	0	2	0	1.6 ± 0.15
<i>Y. periculosa</i>	24	0	0	0	—
<i>N. mezcalaensis</i>	8	0	0	0	—
Open space	4	0	0	0	—
<i>B. gracilis</i>	0	0	0	0	—
<i>C. tehuacanensis</i>	0	0	0	0	—

Notes: Only two saplings survived under *A. constricta* at the end of the experiment, therefore a direct comparison was not possible with the height of saplings grown in the other microhabitat. A. = *Acacia*, B. = *Bouteloua*, C. = *Calliandra*, C. = *Cnidoculus*, E. = *Echinopterys*, L. = *Lippia*, M. = *Mimosa*, N. = *Neobuxbaumia*, P. = *Pseudosmodium*, Y. = *Yucca*.



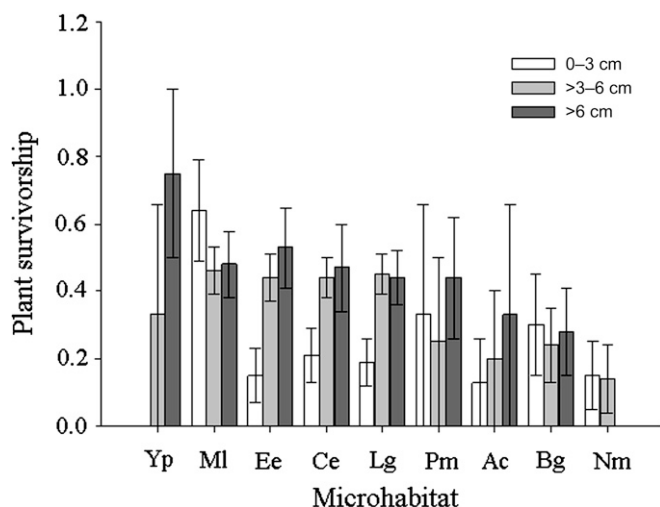


Fig. 1. Survival of *Neobuxbaumia mezcalaensis* juveniles of three height categories, in different microhabitats, three years after initial tagging. Microhabitats: Ac = *Acacia constricta*, Bg = *Bouteloua gracilis*, Ce = *Calliandra eriophylla*, Ee = *Echinopterys eglandulosa*, Lg = *Lippia graveolens*, Ml = *Mimosa lacerata*, Nm = *Neobuxbaumia mezcalaensis*, Pm = *Pseudosmodium multifolium* and Yp = *Yucca periculosa*.

species had a positive effect on the probability of a seed becoming a 12-cm tall juvenile. In contrast, young individuals do not survive in open space, and the rest of the species had little microclimatic effect and/or negative effects on establishment and survival.

Plant performance varied among nurse species exerting positive effects, indicating that not all played the same facilitative role. The highest probabilities occurred beneath the canopies of *L. graveolens*, *M. lacerata*, and *P. multifolium*, while the lowest

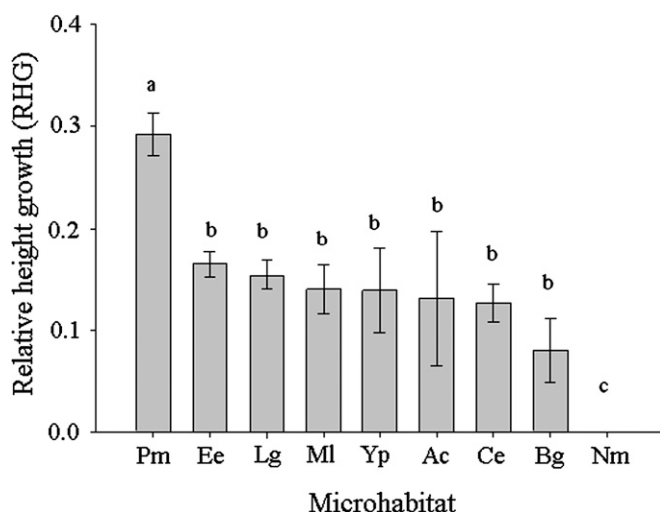


Fig. 2. Relative height growth of juvenile individuals of *Neobuxbaumia mezcalaensis* in the nine microhabitats where *N. mezcalaensis* individuals were observed, including *N. mezcalaensis* (mean  $\pm$  SE). Microhabitats are as in Fig. 1: Ac = *A. constricta*, Bg = *B. gracilis*, Ce = *C. eriophylla*, Ee = *E. eglandulosa*, Lg = *L. graveolens*, Ml = *M. lacerata*, Nm = *N. mezcalaensis*, Pm = *P. multifolium* and Yp = *Y. periculosa*. Relative height growth was estimated during a 3-yr period. Bars not connected with the same letter differ significantly according to a Tukey test ( $\alpha = 0.05$ ).

probabilities were beneath *C. eriophylla*, *E. eglandulosa*, and *A. constricta*. Such differences in the benefits on *N. mezcalaensis* indicate the existence of species-specific facilitative interactions. Our results also show that during the development of the interaction, canopy effects on seedling emergence and differences in growth rates and survivorship become strikingly evident even among morphologically similar nurse species. These species may vary in their shade effects or their effects on soil nutrients and consequently on beneficiary species (see below).

**Microhabitat effect on seed germination**—Seedling emergence occurred after a heavy rain event and was observed in most microhabitats including open space and under *N. mezcalaensis*, which had the lowest percentages. The highest values were observed under most plants with dense canopies, suggesting that seed germination is highly dependent on the microclimatic modification by the nurse architecture, as has been proposed by Drezner (2006). However, the densely canopied *C. tehuacanensis* was a marked exception. There, the absence of germination suggests that other processes such as competition might be much more important than under other densely canopied species, such as reported for the cactus *Trichocereus pasacana* beneath *Baccharis boliviensis*, despite the abundance of seeds in the soil (De Viana et al., 2001). Cazón et al. (2002) found a high inhibitory effect on seed germination by *B. boliviensis* on this cactus. Similar observations have been reported for other disproportionately poor-performing nurse species such as *Larrea tridentata*, which is able to exert strong inhibitory effects on root elongation rates of *Ambrosia dumosa* (McAuliffe, 1988; Mahall and Callaway, 1991, 1992). Although seed predation was high and reduced the number of seeds for germination to 5% of the delivered seeds, a common pattern for many cacti in different environments (Steenbergh and Lowe, 1969, 1977; Turner et al., 1966; Valiente-Banuet and Ezcurra, 1991), this interaction does not occur differentially among microhabitats, indicating that predation does not explain the absence of young individuals under some species.

**Seedling survival and growth after 3 years**—Our results indicate that seedlings in open space cannot survive for more than a month, a pattern reported also for other succulent CAM photosynthetic species such as *Agave deserti* (Jordan and Nobel, 1979), *C. gigantea* (Turner et al., 1966; Steenbergh and Lowe, 1977; Drezner, 2006), *N. tetezo* (Valiente-Banuet and Ezcurra, 1991), and *Mammillaria gaumeri* (Leirana-Alcocer and Parra-Tabla, 1999), indicating that direct sun radiation is deleterious for these CAM plants during early ontogeny. Therefore, survival of *N. mezcalaensis* after 3 years is mostly dependent on microclimatic modifications mostly by densely canopied species, which may be preventing moisture loss and reducing direct sunlight (Castellanos et al., 1999; Drezner and Garrity, 2003; Drezner, 2007). A similar pattern is observed with the cactus *C. gigantea* for which the highest number of individuals associated is related to canopy cover (Drezner, 2006, 2007). However, differences in growth and survival under the densely canopied species, suggest that in addition to microclimatic modifications, species with similar morphologies may vary in their effects on soil nutrients affecting growth rates and survivorship. For example, Carrillo-García et al. (2000a, b) found that soils beneath some species exert an important role for survival and growth of the cactus *Pachycereus pringlei*. These authors found that the higher performance of *P. pringlei* in soil with *Prosopis articulata* in comparison to *Olneya tesota*, is the result of the higher

<i>N. mezcalaensis</i> seeds											
Microhabitat	Ml	Lg	Pm	Ce	Ee	Ac	Yp	Nm	Bg	Ct	os
Seedling emergence	0.21	0.32	0.42	0.50	0.45	0.10	0.10	0.03	0.0	0.0	0.02
Survival after third year	0.42	0.74	0.54	0.05	0.08	0.08	0.0	0.0	0.0	0.0	0.0
Height categories	≤3 cm	0.64	0.19	0.33	0.21	0.15	0.10	0.0	0.15	0.30	0.0
	>3–6 cm	0.46	0.45	0.25	0.44	0.44	0.20	0.33	0.14	0.24	0.0
	>6 cm	0.48	0.44	0.43	0.47	0.53	0.20	0.75	0.0	0.28	0.0
Performance	0.013	0.009	0.008	0.001	0.001	3E-0.5	0.0	0.0	0.0	0.0	0.0

Fig. 3. Overall microhabitat effect on *Neobuxbaumia mezcalaensis* performance in the 11 evaluated microhabitats, showing probabilities for a seed to become a 12 cm high plant and indicating the probability of survival 3 years after the establishment and the survival for each height category in all microhabitats. Microhabitats are as in Fig. 1: Ac = *A. constricta*, Bg = *B. gracilis*, Ce = *C. eriophylla*, Ct = *Cnidoscylus tehuacanensis*, Ee = *E. eglandulosa*, Lg = *L. graveolens*, Ml = *M. lacerata*, Nm = *N. mezcalaensis*, Os = Open space, Pm = *P. multifolium* and Yp = *Y. periculosa*.

percentage of arbuscular mycorrhizae (AM) (Carrillo-García et al., 2000a). This means that positive effects of one species on another can be mediated through fungal intermediaries, although the specific mechanisms contributing to this species-specific nurse relationship is still poorly understood.

Valiente-Banuet and Verdú (2007) found that facilitative interactions occur mostly among distantly related species and that during the ontogeny of the interaction facilitation shifts to competition with increasing taxa relatedness. They suggested that coexistence among distantly related species might possibly be mediated through fungi-mediated resource sharing between different plant species (see Maherali and Klironomos, 2007) or through functional trait complementarity among co-occurring fungal species within patches of vegetation (Valiente-Banuet and Verdú, 2008). Microhabitats that have a positive effect on *N. mezcalaensis* survival (*A. constricta*, *C. eriophylla*, *L. graveolens*, and *M. lacerata*) have been shown to be rich in AM in our study area (Camargo-Ricalde et al., 2003), suggesting a potential role of AM in nurse-beneficiary, species-specific associations.

However, other studies indicate that resource availability may not explain these kinds of patterns. Puerta-Piñero et al. (2006) found that survival and growth of *Quercus ilex* seedlings differed significantly when growing in soils from beneath different species. Interestingly, soils with higher nutrient contents, obtained from beneath *Crataegus* and *Berberis*, did not facilitate seedling performance. In contrast, topsoils with a lower nutrient content (from beneath *Pinus*, in open space, and a sterilized control) greatly benefited plants suggesting a form of interference that probably starts operating several years after the germination.

**Microhabitat effect in survival and growth of previously established plants**—Our results also indicate a relationship be-

tween plant height and survivorship, suggesting that faster growth rates may increase the probability of survival by allowing a more rapid escape from the critical stages of early growth (Steenbergh and Lowe, 1977; Valiente-Banuet and Ezcurra, 1991), which may improve survival rate through increased tolerance to both biotic and abiotic factors (Rey and Alcántara, 2000). In contrast, survivorship tended to be lower in the few individuals already established beneath conspecific adults. In these cases, when plants became taller than 6 cm they died, suggesting that competitive intraspecific exclusion may take several years after establishment for the few individuals that are able to colonize those microhabitats. The lack of growth beneath conspecifics has also been reported for saguaro (McAuliffe and Janzen, 1986), suggesting root competition for water. In fact, although none of the seedlings from the field experiments beneath conspecifics survived more than 50 d after germination, this mortality may be due to low microclimatic effects produced by this short-canopied species as well as to negative effects of conspecifics, which were confounding factors in the experiment.

**Conclusions**—Our results emphasize the importance of analyzing facilitative effects at the community level as a way to assess to what extent the spatial patterns generated by the seed-rain may be kept or modified depending on the nurse plant species and their effects for population dynamics of focal species. Thus, a higher seed-rain directed to poor quality nurse species would reduce the finite rate of population increase, whereas higher seed dispersal directed to high quality nurse species would positively affect population dynamics. For example, Godínez-Alvarez et al. (2002) showed that the finite rate of increase of *N. tetetzo*, a close relative of our study species, is greatly affected by its different frugivore dispersers. They found

that of all the frugivores, the lesser long-nosed bat (*Leptonycteris curasoae*) is the only species that directly disperses toward trees and shrubs, although the authors did not differentiate the nurse species where seeds were placed, nor their quality. These findings emphasize the need to consider the link between the processes of seed dispersal and those of seedling recruitment, considering at least the most abundant nurse species, as has been done here, to fully assess the role of positive and negative interactions on population dynamics of species.

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