Survival and early growth of two congeneric cacti that differ in their level of rarity

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ABSTRACT

In this paper we analyze the growth and early survival of two congeneric columnar cacti: the rare *Neobuxbaumia macrocephala* (with low population densities and a narrow distribution range), and the relatively common *Neobuxbaumia mezcalaensis* (with dense populations and a broader distribution range). Seeds of both species were germinated and seedlings were subjected to different radiation, nutrient and watering treatments in greenhouse conditions for six months. By the end of the experiment seedling average dry mass was similar in both species. Recently emerged seedlings of *N. macrocephala* were smaller than those of *N. mezcalaensis*; however, *N. macrocephala* showed higher relative growth rates (average RGR = 0.0138 mg/mg/day) than *N. mezcalaensis* (average RGR = 0.0126 mg/mg/day). For both species RGR decreased in the shade. Root:shoot ratio (*R/S*) and *K* were higher in *N. mezcalaensis* than in *N. macrocephala* and showed an increasing trend as water availability decreased. Seedling survival was followed in natural conditions for nine months. The survival of *N. mezcalaensis* was significantly higher compared to *N. macrocephala*. In both species a slightly higher seedling survival was observed under the shade of nurse plants. The two species displayed different growth and survival responses, which accounts to some extent for their contrasting level of rarity.

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1. Introduction

The study of rarity as a biological phenomenon is at the core of ecological thinking, because it is unavoidably linked to our understanding of abundance and distribution patterns in nature. Additionally, understanding rarity is important also from the perspective of conservation ecology, as rare species have higher extinction probabilities than common ones and most endangered species show some degree of rarity (Gaston and Kunin, 1997).

The most widely used definition of rarity for plants has been based on three main components: abundance, distribution range and habitat specificity (Rabinowitz, 1981). Esparza-Olguín et al. (2005) proposed that different theoretical frameworks may be used when studying each of these rarity attributes: a) demographic analyses may aid in the study of population numbers; b) meta-population theory may be useful in offering an understanding of a species' geographic distribution range; and c) habitat specificity may be understood by analyzing the species' ecophysiological traits, especially during the early life-cycle phases. Indeed, germination rates and seedling establishment success have been listed among the biological features that may determine the level of rarity of a species (Fiedler and Ahouse, 1992; Bevill and Louda, 1999). Clearly, given that no dispersal limitations exist, the reasons why

a species is present or absent from a certain site are closely linked with the conditions under which seedlings establish most successfully and grow at a faster rate (Bowman and Panton, 1993; Cantin et al., 1997; Cleavitt, 2002; Shimono and Kudo, 2003); thus, analyzing the early survival and growth responses of seedlings to different environmental factors is a central issue in the understanding of rarity. In this paper we analyze the growth responses of two congeneric cacti with contrasting degrees of rarity to different environmental variables, and relate their growth responses to their early survival patterns in natural conditions.

Even though rarity is increasingly recognized as an idiosyncratic and multi-factor phenomenon, the search for general patterns among rare plants is still an important research field, as the documentation of recurrent differences between rare and common plants may allow us to deepen our understanding of rarity and partially compensate for the bias of the published literature toward studies of common taxa (Kunin and Gaston, 1993). In particular, the comparative analysis of closely related species with differing levels of rarity has been a fruitful approach in this field (Bevill and Louda, 1999 and references therein; Gaston and Kunin, 1997; Cleavitt, 2002; Esparza-Olguín et al., 2005; Murray et al., 2005; Ramírez-Padilla and Valverde, 2005; Rodríguez-Pérez, 2005). This approach is based on the premise that the differences between closely related species are not due to lineage effects because they are supposed to have originated relatively recently and have evolved in response to natural selection (Harvey and Pagel, 1991).

It has been proposed that rarity is not evenly distributed among plant families (Gentry, 1986; Fiedler and Ahouse, 1992). While some authors have shown that ancient families tend to have more rare taxa than recent families, other authors have documented differing patterns on different floras (Edwards and Westoby, 2000). Although the Cactaceae is a family of relatively recent origin (ca. 30 million years ago — Hershkovitz and Zimmer, 1997), it certainly contains a high proportion of rare taxa. Yet, the study of rare-common pairs of related species has been an uncommon approach in the study of rarity among cacti; in fact, we know of only three published studies on this area (Esparza-Olguín et al., 2005; Ramírez-Padilla and Valverde, 2005; Ruedas et al., 2006).

Cacti share a number of features in relation to seedling survival and growth. In general, they show low individual growth rates (Steenbergh and Lowe, 1969; Ruedas et al., 2000; Godínez-Alvarez et al., 2003), which determines that seedlings remain vulnerable for long periods of time and makes them prone to high seedling mortality rates, especially as a result of desiccation and predation (Godínez-Alvarez et al., 2003). The stressful conditions that prevail in the arid and semi-arid regions where most cacti are distributed exert limitations to seedling recruitment and often restrict their establishment to microsites under the shade of nurse plants (Godínez-Alvarez et al., 2003; Valverde et al., 2004). Thus, drought is an important abiotic factor contributing to the high seedling mortality observed in many cactus species; in fact, it is thought that species-specific responses to drought are important determinants of their apparent preference for particular edaphic conditions (Ruedas et al., 2006). Although drought is buffered under the shade of nurse plants, the associated decrease in solar radiation (and the concomitant reduction in photosynthetic rate) represents an additional challenge for growth (Martínez-Berdeja and Valverde, 2008). A further strain that cacti seedlings must face is the low nutrient level characteristic of many desert soils. Although slow growing species are generally assumed to be rather indifferent to changing nutrient levels (Chapin et al., 1993), some cacti have shown to be highly responsive to them (Ruedas et al., 2000). Again, the strength of nutrient limitation may decrease under the shade of nurse plants (as the litter produced by them enriches the soil — Nobel, 1980), and also when water availability increases, thus enhancing nutrient availability. Clearly, the effect of the different environmental variables affecting cacti growth is factorial, as they vary simultaneously in time and space.

While these common features may account for similarities in the population dynamics of cactus species, differences in the responses of rare and relatively more common species to their environment may explain variation in their abundance, extent of distribution range, or habitat specificity. In this study we analyze the early survival and growth of two *Neobuxbaumia* species, a rare and a relatively common one, to contribute to our understanding of the factors that determine their differing level of rarity. We conducted a greenhouse experiment to evaluate seedling growth in response to different levels of radiation, watering frequency and nutrient availability, using a factorial design. The latter is an important feature of our experimental approach, as it opens the possibility of evaluating the effect of each factor in isolation, and of the interaction among factors. Additionally, we established an experiment in the field to compare seedling survival in microsites with different levels of shade and evaluate the degree of seedling dependence on the presence of nurse plants. In the field, the two species studied show association with a variety of nurse plants (Ruedas et al., 2006).

2. Materials and methods

2.1. The species studied

a) *Neobuxbaumia macrocephala* (Weber) Dawson is a branched columnar cactus that reaches between 3 and 15 m in height in its adult stage. Between March and July, it produces red–purple flowers on the tip of branches; reproductive branch tips produce a reddish cephalium from which flowers emerge. Flowers are bat pollinated, and seeds (ca. 2.5 mm in diameter and weighting ca. 0.9 mg) are dispersed by bats and birds between April and August Valiente-Banuet et al. (1997). *N. macrocephala* grows in xerophytic shrublands on calcareous soils at altitudes between 1600 and 2300 m and is endemic to the Tehuacán Valley in the state of Puebla. Population densities vary between 130 and 200 individuals per hectare (Ruedas et al., 2006). Here, this species is considered the rarest of the two.

b) *Neobuxbaumia mezcalaensis* (Bravo) Backeberg is an unbranched columnar cactus that may reach between 3 and 14 m in height. Its flowers emerge along the stem between March and May and are white (occasionally green-red) with nocturnal anthesis; they are pollinated by bats. Seeds (ca. 2.5–3 mm in diameter, and weighting 6.0 mg) are dispersed by bats and birds between May and June Valiente-Banuet et al. (1997). This cactus species grows in thorny forests, xerophytic shrublands and tropical dry forests on calcareous soils. It is commonly found at altitudes between 800 and 2000 m, with a geographic distribution range that covers the whole of the Tehuacán-Cuicatlán region (Mexican states of Puebla and Oaxaca), as well as the river Balsas basin (on the southwest of Mexico). Populations are dense, with 1000–17,000 individuals per hectare (Ruedas et al., 2006); thus this species is considered as common.

2.2. The study site

The study consisted of two parts: the first one was carried out in a greenhouse in Mexico City, whereas the second one was a field experiment conducted in the valley of Tehuacán, near Zapotitlán Salinas (18° 20′ North, 97° 28′ West), in the Mexican state of Puebla. This is a semi-arid region covered by a highly diverse xerophytic shrubland. For a detailed description of the area see Valiente-Banuet and Ezcurra (1991), Esparza-Olguín et al. (2002, 2005) and Ruedas et al. (2006).

2.3. Seedling growth analysis in the greenhouse

Seeds of *N. mezcalaensis* and *N. macrocephala* were collected from nine adult individuals per species in June, 2002. After removing them from fruit tissues, seeds were stored in darkness and at room temperature in sterilized glass bottles. In January 2003 (six months after collection) 300 seeds of each species were sown in a tray filled with a 1:1 mixture of tepojal (volcanic sand) and vermiculite. Trays were maintained in a growth chamber with a constant temperature of 25 °C and a photoperiod of 16:8 h (light-dark).

Seed germination took place during the first five days after sowing. Twenty days after germination, 120 seedlings per species were transplanted to 7 × 7 × 6 cm plastic pots (one seedling per pot) filled with the same soil mix described above (the same amount of soil was placed in each pot). Additionally, 15 seedlings per species were harvested, oven dried (at 80 °C for 48 h), and weighted (root and shoot separately) to obtain their dry mass values; these were considered the initial harvest (W_1). The rest of the seedlings (120 per species) were taken to a greenhouse (in Ciudad Universitaria, UNAM, Mexico City) where the growth experiment was conducted.

Immediately after transplanting the seedlings, 55 ml of Peter's nutrient solution (9% N, 45% P and 15% K) were added to each pot. After a 15-day period of acclimatization in the greenhouse, 15 seedlings per species were allocated randomly to each of eight experimental treatments composed from the combination of three

experimental factors: solar radiation, watering frequency, and nutrient availability, each with two levels. The two solar radiation treatments were full exposure to the light conditions of the greenhouse, and a reduction to 40% the full radiation level. In the 100% solar radiation treatment the average PAR at 10:00 am in January, was 189 ± 38 µmol m^{-2} s^{-1}, and in the 40% treatment it was 76 ± 4.7 µmol m^{-2} s^{-1}. The latter treatment was attained by covering each pot with a dark plastic mesh (Ruedas et al., 2000). The two watering treatments consisted in watering each pot with 55 ml of distilled water every week, for the high frequency, or every 15 days for the low frequency treatment. The two nutrient levels were achieved by adding 55 ml of Peter's nutrient solution every month (instead of using distilled water for these watering events) for the high nutrient availability treatment, and watering with distilled water only for the low nutrient availability treatment. In all, the factorial design of the experiment consisted of sixteen treatments: 2 species × 2 nutrient levels × 2 light levels × 2 watering frequencies.

Seedlings were grown under the above conditions for 227 days, from February to July 2003. After this period, they were harvested, oven dried and weighted, roots and shoots separately, to obtain their final dry mass (W_2). W_1 and W_2 were used to calculate the relative growth rate (RGR; Evans, 1972), the root/shoot ratio (R/S) and the allometric coefficient (K) for each species and treatment. Note that W_1 and W_2 correspond to different plant samples: W_1 was obtained from the seedlings in the initial harvest, while W_2 correspond to the plants of the final harvest. The equations used to calculate each growth variable were the following:

$$RGR = (\ln W_2 - \ln W_1)/(t_2 - t_1) \tag{1}$$

$$R/S = W_{roots}/W_{shoot} \tag{2}$$

$$K = RGR_{roots}/RGR_{shoot} \tag{3}$$

The units for RGR were mg/mg/day. Since R/S and K are ratios, they do not have units; in these cases, a value near unity is an indication that the plant allocates similar amounts of biomass to roots and to aerial parts (in the case of R/S), or that the roots grow at a rate similar to that of the shoot (in the case of K).

2.4. Seedling survival in the field

Seedlings used for the field experiment derived from the same seed batch referred to in the previous section (for a detailed report on the seed germination of these species see Ramírez-Padilla and Valverde, 2005). These seedlings were left to grow in the greenhouse under uniform conditions from February to June 2003. Then, 180 seedlings per species were transplanted to the field. Three different types of microsites (treatments) with varying solar radiation levels were selected: 1) exposed; 2) partial shade, under the shade of the shrub *Prosopis laevigata* which has a relatively open canopy; and 3) deep shade, under the shade of *Castella tortuosa*, which has a closed canopy. (We are aware that the use of different nurse species in treatments 2 and 3 implies a mixed effect of shade depth and nurse-plant identity; here we assume that the most important effect of nurse-plant identity is precisely shade depth).

Each treatment was replicated four times ($n = 15$ seedlings per species, per replicate). Seedlings were planted directly on the ground following a 5 × 3 arrangement and spaced at least 2 cm one from the other. When seedlings were planted under the shade of shrubs, they were always located in the northern quadrant of the canopy area as projected on the ground. Seedling survival was monitored monthly for nine months, from July 2003 to March 2004.

To characterize the environmental conditions exerted by the three microsite treatments, the temperature and photosynthetically active radiation (PAR) were measured every 2 h from 12:00 to 18:00 during one day (July 2, 2003). These measurements were averaged to produce a single value per microsite ($n = 4$ replicates per microsite) and analyzed statistically through repeated measures ANOVAs (see Fig. 1).

2.5. Statistical analyses

a) Growth analysis in the greenhouse — Four growth variables were calculated for each species in each of the eight treatments applied: dry mass, relative growth rate (RGR), root:shoot ratio (R/S), and the allometric coefficient (K) (see Appendix for details). The factorial experimental design enabled the use of ANOVA to test the effect of the independent variables (i.e. species, solar radiation, nutrient availability and watering frequency) on the response growth variables. When necessary, the response variables were transformed to logarithm or square root to meet the assumption of normality. Only the experimental factors that had a significant effect on the response variables are illustrated in the Results section.

b) Seedling survival in the field — Seedling survival was expressed as a percentage, as each experimental unit consisted of 15 seedlings (replicated four times), and was analyzed at two
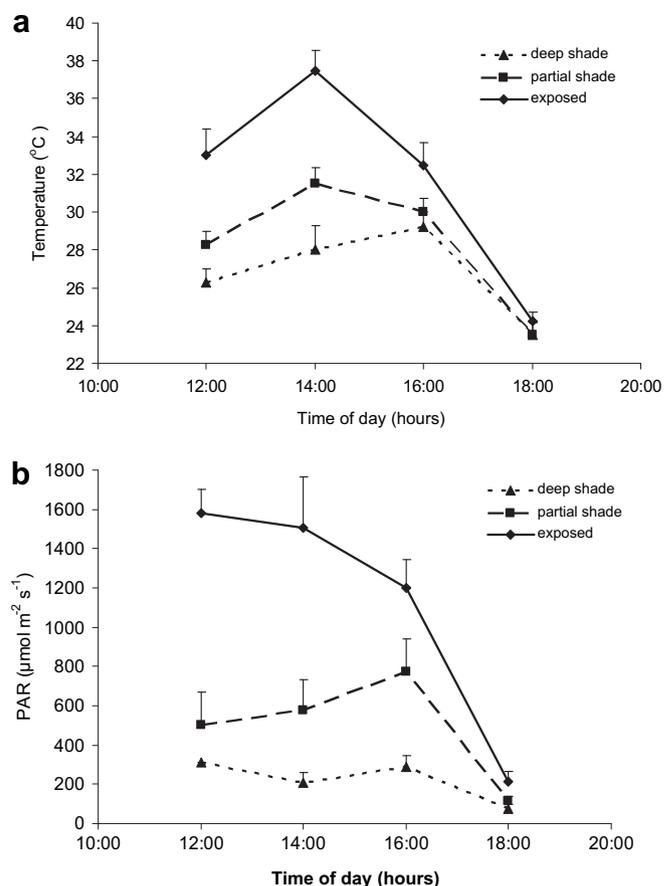

Fig. 1. Environmental characterization of the three field microhabitats in which *Neobuxbaumia* seedlings were planted. a) Shows the temperature variation during a 6-h period, while b) shows the variation in photosynthetically active radiation (PAR). Continuous line = exposed microsites; dashed line = partial shade (under *P. laevigata* trees); dotted line = deep shade (under *Castella tortuosa* shrubs). Error bars are +1 standard error.

times: one month and nine months after the start of the experiment. We used a two-way ANOVA to test the effect of species and microsite on the percentage of seedling survival (see Sork, 1987; Guariguata, 2000 and Holl, 2002 for similar usage of ANOVA for analysis of proportional survival). Percentages were arcsin transformed for normality. Additionally, we used a Peto and Peto log-likelihood ratio test (Pyke and Thompson, 1986) to compare survival curves. We compared the survival curves pairwise, between species in each microsite, and between microsites within each species. A Bonferroni correction was applied to ascertain significant differences between curves.

3. Results

3.1. Growth analysis in the greenhouse

At the end of the experiment, no significant difference in the dry mass values of the two species was detected ($F = 0.89$, $P = 0.34$). However, nutrient addition, radiation and watering frequency had a highly significant effect on dry mass (nutrients: $F = 4.96$, $P = 0.027$; radiation: $F = 152.27$, $P < 0.0001$; watering frequency: $F = 34.28$, $P < 0.0001$).

Additionally, most of the second term interactions were significant (species × nutrients, radiation × nutrients, species × watering, radiation × watering, and nutrients × watering; see Table A1, in the Appendix). The only second term interaction that was not significant was species × radiation ($F = 0.76$, $P = 0.38$), which indicates that both species responded in a similar fashion to the two radiation levels applied. Dry mass values were highest in the 100% solar radiation treatment with frequent watering and nutrient addition, and lowest in the 40% solar radiation treatments for both frequent and sporadic watering, irrespective of nutrient addition (Fig. 2a). Note that Fig. 2a depicts a three-way interaction (between nutrients,

solar radiation and watering frequency) that was not statistically significant ($F = 1.18$, $P = 0.28$); yet, it allows the visualization of all the main effects, as well as most of the two-way interactions, that resulted significant.

The statistical analysis on relative growth rate (RGR) revealed that it varied between species ($F = 19.68$, $P < 0.0001$), and also between solar radiation ($F = 197.75$, $P < 0.0001$) and watering frequency levels ($F = 23.13$, $P < 0.0001$). Additionally, many of the second term interactions were significant (radiation × nutrients, species × watering, radiation × watering; see Table A2, in the Appendix). The species that consistently showed the highest RGR values was *N. macrocephala* (the rare one). The combination of 100% solar radiation and frequent watering resulted in the highest RGR for both species (Fig. 2b). Note, again, that Fig. 2b depicts a three-way interaction (between species, solar radiation and watering frequency) that was not statistically significant ($F = 0.005$, $P = 0.94$); yet, it allows the visualization of all the main effects, as well as some of the two-way interactions, that resulted significant.

The R/S ratio was always below unity for both species and for all treatments, which indicates that more biomass was allocated to the shoots than to the roots. However, there was a significant difference between species ($F = 4.06$, $P = 0.045$), with *N. macrocephala* (rare) generally showing the lowest R/S ratios, i.e. the shoots of *N. macrocephala* were always heavier than those of *N. mezcalaensis* (common), compared to their respective roots. Watering frequency also had a significant effect on R/S ratio ($F = 15.72$, $P = 0.0001$): As expected, seedlings subjected to sporadic watering tended to have higher R/S, compared to those with frequent watering. Finally, the interaction between species, watering frequency and nutrient availability was also significant ($F = 6.70$, $P = 0.01$ — Fig. 2c).

The allometric coefficient, K, refers to the relative growth rate of roots compared to that of shoots. This variable showed great variability in response to the experimental treatments but was always close to unity. Similar to the R/S ratio, K was significantly affected by
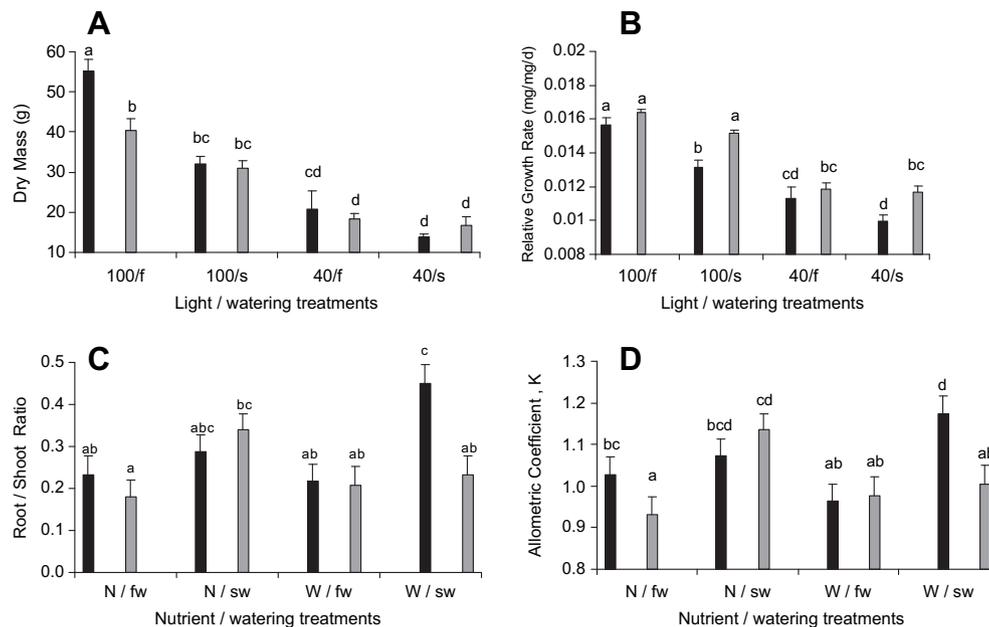

Fig. 2. Effect of experimental factors on the different growth variables measured. In A) dry mass values of both *Neobuxbaumia* species (averaged together) are shown; black bars = added nutrients; grey bars = no nutrients; light and watering treatments (on the x axis) are: 100/f = 100% solar radiation and frequent watering; 100/s = 100% solar radiation and sporadic watering; 40/f = 40% solar radiation and frequent watering; 40/s = 40% solar radiation and sporadic watering. In B) relative growth rate values are given; black bars = *N. mezcalaensis*; grey bars = *N. macrocephala*; light and watering treatments as in panel a). In C) seedling root/shoot ratios (R/S) are shown; dark bars = *N. mezcalaensis*, light bars = *N. macrocephala*; nutrient and watering treatments (on the x axis) are: N/fw = nutrients, frequent watering; N/sw = nutrients, sporadic watering; W/fw = without nutrients, frequent watering; W/sw = without nutrients, sporadic watering. In D) the allometric coefficient values (K) are given; symbols as in panel c). In each panel, bars with different letters are significantly different (P < 0.05, Tukey test). Error bars indicate +1 standard error.

species ($F = 4.99$, $P = 0.027$), watering frequency ($F = 32.78$, $P < 0.0001$) and the interaction between species, watering frequency and nutrient availability ($F = 15.84, P < 0.0001 -$ Fig. 2d). Comparing between species, *N. mezcalaensis* always showed higher K values than *N. macrocephala*. And comparing between watering treatments, frequent watering generally resulted in lower K values than sporadic watering (Fig. 2).

3.2. Seedling survival in the field

The statistical analyses showed that the three types of microsites differed markedly in relation to both temperature and solar radiation. As expected, temperature and PAR fluctuations were more dramatic in the exposed microsites, followed by the partial shade microsites, and finally by the deep shade microsites (Fig. 1).

Seedling survival after one month was relatively high, varying from 67 to 98%. At this early stage, survival differed between species ($F = 8.98$, $P = 0.008$), but not between microsites ($F = 2.74$, $P = 0.091$). *N. mezcalaensis* (common) showed a higher survival (89.1%) than *N. macrocephala* (rare) (71.6%).

In March 2004, nine months after the start of the experiment, overall seedling survival had declined considerably, ranging from 18.3 to 60% (Fig. 3). Again, seedling survival differed between species ($F = 6.01$, $P = 0.0246$), with *N. mezcalaensis* showing the highest survival and *N. macrocephala* the lowest one (51.4% and 22.7% respectively). Although both species showed a tendency toward a lower survival rate under exposed condition, the ANOVA did not detect a significant effect of neither microsite ($F = 0.385$; $P = 0.368$), nor the interaction between species and microsite ($F = 0.053, P = 0.95$) on final seedling survival (Fig. 3).

Regarding the survivorship curve pair-wise comparisons, no differences between microsites, within species, were observed. The only pair-wise comparisons that rendered significant results were between species, in the deep shade and the partial shade microsites, with *N. mezcalaensis* showing a higher survival than *N. macrocephala* in both cases (Table 1).

4. Discussion and conclusions

Our greenhouse experiment results showed that the seedlings of the rare *N. macrocephala* grew at a faster rate than those of the common *N. mezcalaensis*. However, at the end of the experiment
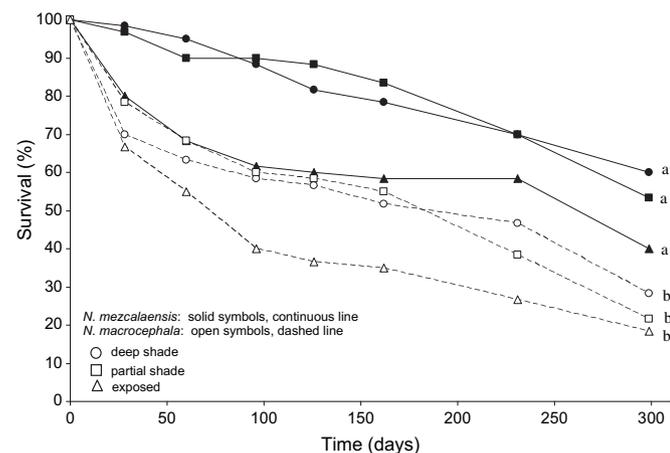
Table 1
Results of the pair-wise comparisons of survivorship curves. The statistical index used is a chi-square (χ^2), with d.f. = 1, according to the Peto and Peto log-likelihood test (Pyke and Thompson, 1986). Values in bold indicate significant differences between survivorship curves (using a Bonferroni correction).

Microsite	χ^2
a) Different microsites for *N. mezcalaensis*	
Deep shade *vs.* partial shade	0.237
Partial shade *vs.* exposed	3.109
Deep shade *vs.* exposed	5.365
b) Different microsites for *N. macrocephala*	
Deep shade *vs.* partial shade	0.277
Partial shade *vs.* exposed	1.418
Deep shade *vs.* exposed	2.283
c) Same microsites between species	
Deep shade *vs.* deep shade	**12.25**
Partial shade *vs.* partial shade	**14.06**
Exposed *vs.* exposed	6.8

the average dry mass of the seedlings of both species was similar. This result may be related to the fact that *N. mezcalaensis* seeds were more than six times heavier than those of *N. macrocephala* (i.e. 6 mg vs. 0.9 mg) and not surprisingly, the recently emerged seedlings of *N. mezcalaensis* were visibly larger than those of *N. macrocephala* (pers. obs). Thus, the slower growing *N. mezcalaensis* produces larger seeds than the faster growing *N. macrocephala*, which support the existence of a negative correlation between seed mass and RGR, as has been suggested by previous studies (Swanborough and Westoby, 1996; Baraloto et al., 2005; Turnbull et al., 2008). The higher RGR of *N. macrocephala* seedlings allowed them to reach a similar size (i.e. dry weight) to those of *N. mezcalaensis* after six months in the greenhouse. Yet, even if *N. macrocephala* seedlings are capable of eventually overcoming their initial size disadvantage, they must face an initial period of increased vulnerability (compared to *N. mezcalaensis*) in the field that may have important consequences in terms of survival probabilities, as will be discussed below.

A smaller seed size in rarer compared to more common species is not an unusual occurrence, and has even been used to explain relative rarity among closely related species (Brown et al., 2003). Indeed, our results suggest that the difference in seed size (and therefore early seedling performance) could account to some extent for the difference in abundance between the two species studied, at least at the location at which our filed study was carried out. The larger seeds of the common *N mezcalaensis* may be related to its higher abundance compared to the small-seeded *N. macrocephala*. In addition, the relative performance of the early life-cycle stages of these two species could depend on soil characteristics and other environmental features, and could therefore vary from location to location, giving place to their distinct habitat occupancy patterns (Esparza-Olguín et al., 2005; Ruedas et al., 2006). The rare *N. macrocephala* is restricted to relatively uncommon habitats (Ruedas et al., 2006), and the growth adaptations that make this species successful in its restricted habitats may represent a cost and decrease its success in more common habitats (Poot and Lambers, 2003).

On the other hand, it has been found that rare species restricted to particular substrates grow at slower rates than their widespread congeners (Fiedler, 1987). In this study we have found the exact opposite trend, as the rare *N. macrocephala* showed a consistently higher RGR than the more widespread *N. mezcalaensis* in all the experimental conditions tested.

Regarding the experimental factors (analyzed as main effect) that affected the growth response of the *Neobuxbaumia* species analyzed, it was noteworthy that solar radiation and watering frequency had a significant effect on most growth variables. On the

Fig. 3. Survivorship curves of *Neobuxbaumia mezcalaensis* (continuous lines, solid symbols) and *N. macrocephala* (dotted lines, open symbols) seedlings during 300 days in the field under different microhabitats: circles = deep shade; squares = partial shade; triangle = exposed microsites. Lines with different letters show significant differences in final proportional survival ($P < 0.05$, Tukey test).

other hand, nutrient addition had a significant effect only on dry mass. The relevance of water availability during the early life-cycle stages of cacti and other desert plants has been widely documented (Nobel, 1980; Jordan and Nobel, 1981; Martínez-Berdeja and Valverde, 2008) and thus the positive response of *Neobuxbaumia* seedlings to water addition was not a surprising result. On the other hand, the exposure to full solar radiation is usually thought to be detrimental (Godínez-Álvarez and Valiente-Banuet, 1998; Ruedas et al., 2000). In fact, the positive role played by nurse plants in reducing high solar radiation levels and increasing seedling survival is well known (Gibson and Nobel, 1986; Valiente-Banuet and Ezcurra, 1991; Flores-Martínez et al., 2004). Yet, opposite results have been found for other cacti that are rather insensitive to contrasting radiation levels (Martínez-Berdeja and Valverde, 2008). Surprisingly, our results showed that high solar radiation levels were actually positive for the growth of the *Neobuxbaumia* seedlings analyzed. This coincides with the general expectation that higher radiation levels will result in higher growth rates, given that enough humidity is available for photosynthesis (Taiz and Zeiger, 2002). Indeed, *Neobuxbaumia* seedlings showed an increase in relative growth rate and seedling biomass under full sunlight compared to 40% solar radiation. However, it is worth noting that the PAR values in the greenhouse where the experiment was carried out were much lower than those experienced under natural conditions. Therefore, the effect of real field radiation levels on the growth of *Neobuxbaumia* seedlings remains to be tested more fully (our field results measured survival, but not growth). However, experimental evidence published by other authors working with another *Neobuxbaumia* species suggests that high solar radiation levels could indeed be detrimental for seedling growth (Godínez-Álvarez and Valiente-Banuet, 1998).

Regarding nutrient addition, our greenhouse experiment results showed that, when analyzed in isolation, it had a significant effect on dry mass, but not on RGR, or R/S, or K. However, nutrients were involved in several two-way and three-way significant interactions. For instance, a three-way significant interaction was found between species, watering frequency and nutrient addition on R/S and K. That is, the effect of nutrient addition varied depending on watering frequency and on the species involved: lower R/S and K values were obtained when plants were watered frequently, this effect being more noticeable in *N. macrocephala* but only when nutrients were added; when nutrients were not added, the species that was more responsive to watering frequency was *N. mezcalaensis*.

A limited response to increased nutrient availability, along with low RGR values, are common features of species that have evolved in stressful environments (Grime and Campbell, 1991). The relatively low RGR values shown by *N. mezcalaensis* and *N. macrocephala* are indeed shared with other species in the Cactaceae (Godínez-Alvarez et al., 2003; Martínez-Berdeja and Valverde, 2008).

The results of the field experiment showed that the common *N. mezcalaensis* consistently had a higher seedling survival than *N. macrocephala*. The initial relative advantage of *N. mezcalaensis* seedlings (given their larger size) could have been an important factor accounting for the differences in survival observed between the two species in the field, and these, in turn, may contribute to the higher abundance — and relative commonness — of *N. mezcalaensis*.

The higher survival rate of *N. mezcalaensis* seedlings in the field compared to *N. macrocephala*, could have been related also to its relatively higher root allocation and higher root relative growth rate, as expressed by the high R/S and K values observed in the greenhouse experiment. As both species inhabit arid lands in which water availability is critical for seedling establishment, it is easy to envisage why the quick development of a strong and efficient root system would be of great importance in determining seedling fate. The higher R/S and K values of the common *N. mezcalaensis* and its ability to respond to water availability (and to some degree to nutrient addition, given the significant interaction between species, watering frequency and nutrient addition) by varying both R/S and K, suggest that this species is capable of developing a strong root system that may represent an important advantage for water and nutrient collection and storage during the early developmental phases. Contrary to our findings, other authors have reported that when comparing rare and common congeneric species, it was precisely the rare species that produced the highest R/S values, and not the common ones (Poot and Lambers, 2003).

Note that, although a general tendency was observed in both species toward higher survival in shaded than in exposed conditions, no significant effect of microhabitat was observed on seedling survival after nine months. The lack of a clearer positive effect of nurse plants on survival was an unexpected result, given that most studies on columnar cacti have reported a dramatic increase in survival under the protective shadow of shrubs (Valiente-Banuet and Ezcurra, 1991; Flores-Martínez et al., 2004). It is worth mentioning that the period of our field experiment (from July 2003 to March 2004) was exceptional compared to other years in many ways: the rainy season was longer than usual, the total rainfall was well above average, and the distribution of rainfall events was relatively even in time (pers. obs.). These relatively beneficial conditions must have contributed to the unremarkable difference in seedling survival between the different microsites.

Our study has shown that the understanding of the performance of the early life-cycle stages of related species may shed light on the environmental and biological factors that can determine their relative rarity or commonness. For this particular system of congeneric species a host of information is now available that indicates that rarity and commonness are multi-factor phenomena in which all the subjects that have been addressed (i.e. demography, germination behavior, habitat specificity and seedling growth responses) have a part to play (Esparza-Olguín et al., 2005; Ramírez-Padilla and Valverde, 2005; Ruedas et al., 2006).

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Appendix

Detailed statistical results of the factorial ANOVAs performed to analyze the effect of experimental factors on the growth variables considered.

Table A1. Results of the ANOVA performed on the dry mass (g) of *Neobuxbaumia* seedlings. In all cases, the degree of freedom (d.f.) of the effect is 1, and the degrees of freedom (d.f.) and mean square (M.S.) of the error term are 202, and 173.61, respectively. The main effects are species (1), light (2), nutrients (3) and watering frequency (4). Significant effects ($P < 0.05$) are shown in bold in the P-value column.

Effect	M.S. effect	F	P-value
1	155.74	0.897	0.3447
2	26435.65	152.266	**<0.0000**
3	861.76	4.963	**0.0270**
4	5951.10	34.278	**<0.0000**
1,2	131.88	0.759	0.3845
1,3	755.19	4.350	**0.0383**
2,3	847.81	4.883	**0.0282**
1,4	1123.26	6.470	**0.0117**
2,4	2011.27	11.584	**0.0008**
3,4	1261.12	7.263	**0.0076**
1,2,3	15.78	0.091	0.7633
1,2,4	0.04	0.0002	0.9883
1,3,4	126.77	0.730	0.3938
2,3,4	204.62	1.178	0.2789
1,2,3,4	26.45	0.152	0.6966

Table A2. Results of the ANOVA performed on the relative growth rate (RGR) of *Neobuxbaumia* seedlings. In all cases, the degree of freedom (d.f.) of the effect is 1, and the degrees of freedom (d.f.) and mean square (M.S.) of the error term are 202, and 0.0000041, respectively. The main effects are species (1), light (2), nutrients (3) and watering frequency (4). Significant effects ($P < 0.05$) are shown in bold in the *P*-value column.

Effect	M.S. effect	F	P-value
1	0.000082	19.682	**<0.0000**
2	0.000820	197.750	**<0.0000**
3	0.000004	1.048	0.3073
4	0.000096	23.134	**<0.0000**
1,2	0.000001	0.161	0.6884
1,3	0.000007	1.676	0.1969
2,3	0.000019	4.536	**0.0344**
1,4	0.000021	4.954	**0.0271**
2,4	0.000017	4.013	**0.0465**
3,4	0.000006	1.355	0.2458
1,2,3	0.000002	0.569	0.4513
1,2,4	0.000000	0.005	0.9412
1,3,4	0.000000	0.044	0.8333
2,3,4	0.000006	1.517	0.2195
1,2,3,4	0.000001	0.227	0.6344

Table A3. Results of the ANOVA performed on the root/shoot ratio of *Neobuxbaumia* seedlings. In all cases, the degree of freedom (d.f.) of the effect is 1, and the degrees of freedom (d.f.) and mean square (M.S.) of the error term are 202, and 0.047, respectively. The main effects are species (1), light (2), nutrients (3) and watering frequency (4). Significant effects ($P < 0.05$) are shown in bold in the *P*-value column.

Effect	M.S. effect	F	P-value
1	0.19058	4.060	**0.0452**
2	0.04243	0.904	0.3429
3	0.00722	0.154	0.6954
4	0.73791	15.721	**0.0001**
1,2	0.03237	0.690	0.4073
1,3	0.16476	3.510	0.0624
2,3	0.10928	2.328	0.1286
1,4	0.02503	0.533	0.4661
2,4	0.14962	3.188	0.0757
3,4	0.00244	0.052	0.8198
1,2,3	0.02716	0.579	0.4477
1,2,4	0.11013	2.346	0.1272
1,3,4	0.31445	6.699	**0.0103**
2,3,4	0.01376	0.293	0.5888
1,2,3,4	0.0029	0.062	0.8039

Table A4. Results of the ANOVA performed on *K* (the allometric coefficient) of *Neobuxbaumia* seedlings. In all cases, the degree of freedom (d.f.) of the effect is 1, and the degrees of freedom (d.f.) and mean square (M.S.) of the error term are 198, and 0.0236, respectively. The main effects are species (1), light (2), nutrients (3) and watering frequency (4). Significant effects ($P < 0.05$) are shown in bold in the *P*-value column.

Effect	M.S. effect	F	P-value
1	0.118	4.988	**0.0266**
2	0.005	0.205	0.6512
3	0.008	0.319	0.5729
4	0.775	32.777	**<0.0000**
1,2	0.002	0.105	0.7460
1,3	0.048	2.036	0.1552
2,3	0.078	3.286	0.0714
1,4	0.002	0.076	0.7834
2,4	0.017	0.711	0.4002
3,4	0.001	0.025	0.8735
1,2,3	0.005	0.229	0.6328
1,2,4	0.051	2.155	0.1437
1,3,4	0.375	15.841	**0.0001**
2,3,4	0.022	0.919	0.3388
1,2,3,4	0.072	3.061	0.0818

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