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Growth response of three globose cacti to radiation and soil moisture: An experimental test of the mechanism behind the nurse effect

Alejandra Martínez-Berdeja, Teresa Valverde *

Grupo de Ecología de Poblaciones, Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México, Ciudad Universitaria, Mexico D.F. 04510, Mexico

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ABSTRACT

Cactus seedlings often establish under nurse plants which modify environmental conditions by increasing moisture and decreasing solar radiation, which may cause beneficial and detrimental effects, respectively, on seedling growth. Three soil moisture treatments (5%, 25% and 60%) and two solar radiation levels (100% exposure = 243 $\mu mol\, m^{-2}\, s^{-1}$, and 40% = 102 $\mu mol\, m^{-2}\, s^{-1}$) were used in a factorial design to analyze seedling growth response of three rare cactus species (*Mammillaria pectinifera*, *Obregonia denegrii* and *Coryphantha werdermannii*). The variables evaluated were relative growth rate (RGR), root/shoot ratio (*R*/*S*), and *K* (RGR_{roots}/RGR_{shoot}), obtained from an initial seedling harvest (6-month-old seedlings) and a final harvest 6 months after treatment application. All three species had slow RGRs (0.002–0.012 $g\, g^{-1}\, day^{-1}$). *O. denegrii* had the lowest RGR values, but was the only species for which *R*/*S* and *K* varied with soil moisture. While all seedlings responded markedly to soil moisture, no response was observed to radiation treatments. The latter might have been related to the relatively low solar radiation levels present in the greenhouse. Yet, our results suggest that the main benefit nurse plants offer to seedlings is the increase in soil moisture.

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1. Introduction

As in most plant species, population dynamics in cacti are strongly dependent on seedling recruitment. However, the dynamics of early life-cycle stages in arid environments differ dramatically from those of other species from temperate or tropical habitats. Since most cacti inhabit arid environments, they face extremely stressful conditions from very early in life. Among these stressors are low water availability, intense solar radiation, and widely fluctuating temperatures (Leirana-Alcocer and Parra-Tabla, 1999; Steenbergh and Lowe, 1969; Valiente-Banuet and Ezcurra, 1991). These conditions, along with low nutrient availability and herbivory, result in high seedling mortality in cactus populations (Contreras and Valverde, 2002; Esparza-Olguín et al., 2002; Godínez-Álvarez et al., 2003; Mandujano et al., 1998; Steenbergh and Lowe, 1969). In addition, due to their slow growth rate, cactus seedlings may be highly vulnerable for much longer than other plant species. Thus, the selective pressure favoring fast growth rates must be strong, since the probability of survival is determined by the amount of storage tissue developed during early growth (Jordan and Nobel, 1981).

* Corresponding author. Tel.: +52 55 56 22 49 12; fax: +52 55 56 22 48 28.
E-mail address: mtvv@hp.fciencias.unam.mx (T. Valverde).

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Cacti are generally considered to be "stress tolerant" plants (sensu Grime, 1977) that have evolved in environments where the availability of one or several resources is limiting. As such, they are expected to have slow relative growth rates (RGRs) and reduced phenotypic plasticity (Chapin et al., 1993; Grime et al., 1986; Lambers and Poorter, 1992). The phenotypic plasticity of stress tolerant plants is generally expressed in physiological rather than morphological traits (e.g., in RGR, rather than changes in the root/shoot ratio), and this physiological plasticity, though limited compared to fast-growing species, allows them to exploit temporary and unpredictable pulses in resource availability (Grime et al., 1986; Nobel, 1988).

Most deserts and semi-deserts receive little rain annually, which falls episodically and seasonally. Therefore, seed germination in cactus populations can only occur during the short windows of opportunity that are associated with the onset of the rainy season (Contreras and Valverde, 2002; Esparza-Olguín et al., 2002; Flores et al., 2004; Franco and Nobel, 1989; Valiente-Banuet and Ezcurra, 1991; Valverde and Zavala-Hurtado, 2006). Furthermore, seedling establishment is limited not only temporally but also spatially, being restricted to microsites beneath nurse plants that buffer variations in temperature, solar radiation, moisture, and other factors (Jordan and Nobel, 1981; Leirana-Alcocer and Parra-Tabla, 1999; Valiente-Banuet and Ezcurra, 1991). The introduction of the nurse plant concept was an important contribution to our understanding of the ecology of arid and semi-arid environments, since it emphasized the role of positive interactions in community structure and function. Yet, there are still several aspects of the seedling–nurse interaction that remain unclear. For example, the presence of a nurse plant modifies environmental conditions in ways that may have opposing effects on the growth of the nursed seedlings; a reduction in evapo-transpiration and temperature buffering may be beneficial (Flores et al., 2004; Gibson and Nobel, 1986; Valiente-Banuet and Ezcurra, 1991), while increased competition levels (i.e., with the nurse plant—Flores-Martínez et al., 1994) and decreased solar radiation (considered only in terms of the energy available for photosynthesis) may be detrimental (Franco and Nobel, 1989). While several authors have addressed this subject through field experiments, the limitation of such an approach is that the effects of different ecological factors remain confounded (Franco and Nobel, 1989; Valiente-Banuet and Ezcurra, 1991). In contrast, experimentation under controlled conditions allows one to separate the effects of the different factors involved. Additionally, it is particularly difficult to assess the effect of soil moisture as an experimental factor in the field, while under controlled conditions it may be effectively evaluated.

A small number of studies have experimentally examined the effect of solar radiation on the growth of cactus seedlings with the aim of understanding the role played by the nurse plant. Although traditional growth analyses based on biomass accumulation rate have seldom been performed with cactus species, the few results available suggest that seedlings may achieve higher growth rates under the shade than in direct sunlight (Carrillo-García et al., 2000; Flores et al., 2004; Godínez-Álvarez and Valiente-Banuet, 1998; Nolasco et al., 1997; Ruedas et al., 2000). However, the reduced growth rates of seedlings in direct sunlight seem counterintuitive given the current knowledge on the biochemistry of photosynthesis, which indicates that higher radiation levels would generally result in higher growth rates (Taiz and Zeiger, 2002). Moreover, in most cases, one is left wondering whether the seedlings indeed responded to the effect of reduced solar radiation, or they grew faster because of the increased moisture levels in the shaded microsites given that in most experiments these two factors are not addressed separately. In addition, in most of the cases cited, the experimental set-up included enough water to guarantee the survival of the plants. So, the effect of water limitation has seldom been addressed in a detailed manner (but see Flores, 2001), and neither has the interaction between water availability and solar radiation.

To deepen our understanding of the effect of nurse plants on the growth of cactus seedlings, we analyzed the growth response of the seedlings of three cactus species: *Mammillaria pectinifera*, *Obregonia denegrii* and *Coryphantha werdermannii* to different levels of solar radiation and soil moisture. We applied a factorial experimental design to test the effect of each experimental factor separately, as well as the interaction between them. Our hypotheses were that (1) all three species would have low RGRs and a limited plasticity (i.e., changes in biomass allocation patterns) in response to variations in solar radiation and soil moisture; (2) for the three species, the highest RGR values would occur in the high water availability and high solar radiation treatment; and (3) the seedlings would respond to moisture more notably than to radiation, given that water is the main limiting factor in semi-arid ecosystems. The three cactus species have a globose life form, which allows us to compare them in terms of their growth responses, since there is evidence that growth patterns are related to life form in cacti and other desert plants (Flores, 2001; Flores et al., 2004).

2. Materials and methods

2.1. The studied species

All three species have a small distribution range and small populations. These features have determined their inclusion in the Mexican endangered species list (NOM-059-SEMARNAT-2001). *O. denegrii* is also in the IUCN Red List (Anderson et al., 2002). All three species are also listed in Appendix I of CITES (Hunt, 1992), owing to their high ornamental value among collectors.

2.1.1. *Mammillaria pectinifera Weber*

This species is endemic to the Tehuacán Valley in the Mexican state of Puebla (for details of the area see Valverde and Zavala-Hurtado, 2006). This plant is a small, solitary globose cactus ca. 5–8 cm in diameter; its shoot is composed of conic

tubercules covered with short, radial and pectinated spines. Its roots are fibrose and its flowers are pale pink in color, and emerge between November and February (Bravo-Hollis and Sánchez-Mejorada, 1991). Little is known about the ecological conditions required for seedling establishment in this species. Some authors have observed seedlings of *M. pectinifera* in open spaces, from which they conclude that it does not require the protection of a nurse plant (Rodríguez-Ortega and Ezcurra, 2000; Zavala-Hurtado and Valverde, 2003). However, it has also been reported to establish under the shade of *Salvia* sp., *Jatropha dioica* and *Acacia subangulata* (Rodríguez-Ortega and Ezcurra, 2000). In addition, since the seeds of *M. pectinifera* are dispersed close to their mother plants, the latter may function as nurse plants for emerging seedlings (Valverde and Zavala-Hurtado, 2006). The same kind of protection may be provided by the abundant rocks on the ground where this species lives (Martorell and Peters, 2005). Finally, as *M. pectinifera* shows a hemigeophytic growth habit (i.e., it grows semi-buried in the ground), seedlings may be partially covered by the soil, which may protect them from solar radiation (H. Godínez-Álvarez, personal communication).

2.1.2. *Obregonia denegrii Fric*

This species is endemic to the Jaumave Valley in the Mexican state of Tamaulipas (for details of the area see Martínez et al., 1994). It is a small subglobose cactus with triangular tubercules which form a rosette; each tubercule bears three or four spines. Its roots are fusiform and are able to store water. This plant produces white flowers during spring and summer (Bravo-Hollis and Sánchez-Mejorada, 1991). There is no published information available regarding the conditions required for *O. denegrii* seedlings to establish, but several researchers agree that it germinates and grows in shaded microsites (J. Reyes-Santiago, personal communication; M.C. Mandujano, personal communication).

2.1.3. *Coryphantha werdermannii Boedeker*

This species is endemic to the Mexican state of Coahuila (Cuatro Ciénegas and Cerro de la Paila localities—for details of the area see Badino et al., 2004). It is a solitary globose cactus, ca. 6 cm in diameter, with pyramidal tubercules bearing 15–20 radial, acicular, sturdy spines (Bravo-Hollis and Sánchez-Mejorada, 1991). Its flowers are yellow and are produced during June and July. No published information is available regarding the conditions needed for its seedlings to establish. Some researchers report that it establishes in fully exposed microsites (C. Martorell, personal communication), while others insist that it establishes in the shade of rocks and other abiotic elements (M. Portilla-Alonso, personal communication).

2.2. *Growth experiment under controlled conditions*

The seeds of each species were germinated on filter paper in Petri dishes which were placed in a growth chamber with a 12 h temperature cycle (18–32 °C) and a 12:12 h photoperiod. Emerging seedlings were transplanted to $6 \times 5.5 \times 5\,cm^3$ pots (one seedling per pot) filled with 160 g of dry soil (black soil with volcanic gravel and sand, 2:1). Pots were initially watered with 55 ml of Peters solution (9% nitrogen, 45% phosphorus and 15% potassium) and subsequently with tap water (twice a week) to keep the soil at a relative moisture level of approximately 50% (see details below). Seedlings were acclimatized in a greenhouse in Mexico City for 5 months (April–August, 2005). Ten seedlings of each species were then harvested, aerial and root organs were separated and oven dried at 80 °C for 48 h, and their dry weight was obtained.

The remaining seedlings were subjected to a factorial experiment for a 6-month period (September, 2005–February, 2006) in the same greenhouse. The experimental design consisted of six treatments resulting from the combination of two experimental factors: solar radiation (with two levels: 100% and 40%) and soil moisture (with three levels: 60%, 25% and 5%). The two radiation levels were achieved by loosely fitting plastic lids above each pot. Lids were either transparent (100% solar radiation) or covered with a mesh which only allowed 40% of the solar radiation through. Average PAR measured with a quantum meter placed below these lids was $243\,\mu mol\,m^{-2}\,s^{-1}$ for the 100% treatment, and $102\,\mu mol\,m^{-2}\,s^{-1}$ for the 40% treatment (on a warm May day, between 11:00 and 15:00 h). Although the radiation levels present in the greenhouse were lower than those experienced by the studied species in their semi-desert environment, we assumed that the specific PAR levels used were of secondary importance compared to the contrast between them, since the main aim of our study was to understand the response of plants to contrasting light conditions (the implications of this decision are addressed in Section 4).

The three levels of soil moisture were achieved by watering each pot every other day up to its assigned moisture level (relative water content, i.e., 5%, 25% and 60% water by weight). To obtain relative water content, first we watered each pot to field capacity, then we waited for 2 h after the excess water had stopped draining out and weighed each pot to the nearest dg. The mass corresponding to the soil and the pot were subtracted from the total mass to obtain the water mass contained in each pot, the latter corresponding to 100% relative water content. Once this value was known, we calculated the mass that would correspond to 5%, 25%, or 60% water content, and waited for the pots to dry until the desired weight was reached. Subsequently, the plants were watered every other day to maintain the required weight which was verified by weighing each pot.

The relative water contents of 5%, 25% and 60% resembled the soil water potential levels recorded in semi-arid regions in Mexico before, during and after the rainy season, and may also represent the water potential of open microsites (5%) and those underneath nurse plants (25%). The two radiation levels (40% and 100%) were intended to simulate the light conditions in the open and under nurse plants. Even though the radiation and soil water potential values applied in this

experiment may not correspond to the exact values encountered by these species in nature, the difference between treatments allowed us to analyze the growth response of each species to the contrasting conditions they may face in the field.

We used a minimum of seven seedlings (i.e., replicates) per species, per treatment. For *O. denegrii*, only two soil moisture treatments were applied (25% and 60%) because the number of seeds available was limited. During the experiment, pot location on the greenhouse table was randomized every 2 weeks.

2.3. Data analysis

The seedlings were harvested in February, 2006, 6 months after the start of treatment application. Seedlings were oven dried (48 h at 80 °C) and weighed to obtain the final dry weights (W), from which the following growth variables were derived:

$$\text{relative growth rate,} \quad \mathrm{RGR} = \frac{\ln W_f - \ln W_i}{t_f - t_i}, \tag{1}$$

$$\text{root/shoot ratio,} \quad \frac{R}{S} = \frac{W_{\text{roots}}}{W_{\text{shoot}}}, \tag{2}$$

$$K = \frac{\mathrm{RGR}_{\text{roots}}}{\mathrm{RGR}_{\text{shoot}}}, \tag{3}$$

where the sub-indexes f and i refer to the final and the initial harvest values, respectively (Evans, 1972). 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).

Two sets of statistical analyses were performed: (a) one which included the three species and only two soil moisture levels (since one of the moisture levels, 5%, was not applied to all three species); and (b) another which was carried out per species and included all the treatments applied to each species. For (a), an unbalanced three-way ANOVA was performed on the growth variables (RGR, R/S and K). The explanatory factors were species (three levels: *M. pectinifera*, *O. denegrii* and *C. werdermannii*), soil moisture (two levels: 60% and 25%); and solar radiation (two levels: 100% and 40%). Some variables had to be log transformed prior to analysis to meet the assumptions of normality. For (b), an unbalanced two-way ANOVA was carried out for each species, with the explanatory factors being soil moisture (three levels for *M. pectinifera* and *C. werdermannii*: 60%, 25% and 5%, and two levels for *O. denegrii*: 60% and 25%), and solar radiation (two levels: 100% and 40%).

3. Results

The results are presented in two sections: (a) the comparison of the growth response of the three species to the treatments that were applied to all of them (i.e., 25% and 60% soil moisture, and 40% and 100% solar radiation); and (b) the detailed growth parameters obtained per species.

3.1. Growth response of the three species

The results of the three-way ANOVA showed that solar radiation did not have a significant effect on any of the growth variables obtained (RGR: $F = 0.28$, d.f. $= 1,70$, $P = 0.6$; R/S: $F = 1.00$, d.f. $= 1,70$, $P = 0.32$; K: $F = 0.97$, d.f. $= 1,66$, $P = 0.97$) (Table 1). The effect of soil moisture, however, was highly significant for all variables (RGR: $F = 13.94$, d.f. $= 1,70$, $P < 0.001$; R/S: $F = 8.19$, d.f. $= 1,70$, $P = 0.005$; K: $F = 20.41$, d.f. $= 1,66$, $P < 0.001$) (Table 2) and in all species, higher soil moisture resulted in higher RGR values, and lower R/S and K values (Table 2). Finally, the species factor was also significant for the three variables (RGR: $F = 3.24$, d.f. $= 2,70$, $P = 0.045$; R/S: $F = 36.25$, d.f. $= 2,70$, $P < 0.0001$; K: $F = 46.99$, d.f. $= 2,66$, $P < 0.001$). *M. pectinifera* had the highest RGR values, while the lowest were recorded for *C. werdermannii* (Table 3). On the other hand, *O. denegrii* had the highest R/S and K values, while *C. werdermannii* had the lowest values for these variables (implying a relatively low root weight and low root growth rate, compared to the values for the shoot—Table 3).

Table 1
Average values (±1 S.D.) for the different growth variables analyzed in the two solar radiation treatments applied to all the species

Solar radiation	W	RGR	R/S	K
40%	0.019±0.017	0.010±0.004	1.616±0.364	1.523±0.715
100%	0.017±0.015	0.009±0.004	1.565±0.381	1.504±0.964

W, dry weight; RGR, relative growth rate; R/S, root/shoot ratio; K, $\mathrm{RGR}_{\text{root}}/\mathrm{RGR}_{\text{shoot}}$.

Table 2
Average values (±1 S.D.) for the different growth variables analyzed in the two soil moisture treatments applied to all the species

Soil moisture	*W*	RGR	*R*/*S*	*K*
25%	0.013±0.017 a	0.008±0.004 a	0.68±0.364 a	1.83±0.715 a
60%	0.023±0.015 b	0.018±0.004 b	0.501±0.381 b	1.20±0.964 b

W, dry weight; RGR, relative growth rate; *R*/*S*, root/shoot ratio; *K*, RGR_{root}/RGR_{shoot}. Different letters in each column indicate significant differences ($P<0.05$) between means according to the Tukey HSD test.

Table 3
Average values (±1 S.D.) per species for the different growth variables analyzed

Species	*W*	RGR	*R*/*S*	*K*
M. pectinifera	0.032±0.021 a	0.011±0.005 a	0.427±0.221 a	1.451±0.677 a
O. denegrii	0.010±0.005 b	0.008±0.003 b	0.946±0.4 b	2.191±0.926 b
C. werdermannii	0.013±0.007 b	0.009±0.003 ab	0.405±0.151 a	0.938±0.23 c

Nomenclature for variables and statistical results as in Table 2.

Table 4
Average values (±1 S.D.) for the different growth variables analyzed in the different soil moisture treatments for each species

Species	Soil moisture (%)	*W*	RGR	*R*/*S*	*K*
M. pectinifera	5	0.013±0.006 a	0.007±0.003 a	0.496±0.206	2.961±0.082
	25	0.023±0.018 ab	0.008±0.005 ab	0.425±0.248	1.634±0.904
	60	0.041±0.020 b	0.012±0.004 b	0.429±0.201	1.296±0.376
O. denegrii	25	0.008±0.002 a	0.007±0.002 a	1.106±0.353 a	2.775±0.895 a
	60	0.012±0.005 b	0.009±0.003 b	0.774±0.388 b	1.51±0.256 b
C. werdermannii	5	0.003±0.001 a	0.002±0.002 a	0.292±0.232	1.031±0.512
	25	0.011±0.006 b	0.008±0.003 b	0.491±0.167	1.04±0.278
	60	0.016±0.007 b	0.011±0.003 b	0.319±0.058	0.835±0.01

Nomenclature for variables and statistical results as in Table 2. Tukey HSD tests for which statistical results are reported were performed per species.

The only interaction between factors that appeared important was the soil moisture × species interaction which was highly significant for *K* ($F = 4.10$, d.f. = 2,66, $P = 0.02$) and marginally significant for *R*/*S* ($F = 2.94$, d.f. = 2,70, $P = 0.06$) (Table 4). That is, the way in which *K* and *R*/*S* varied in response to soil moisture was dependant upon species: in *O. denegrii*, the response to the two soil moisture levels was very contrasting, while for the other two species the difference between the two treatments was not as dramatic (Table 4). The interaction between soil moisture and species was not significant for RGR ($F = 0.80$, d.f. = 1,70, $P = 0.37$).

3.2. Growth response per species

A general result of these analyses was that solar radiation did not have any significant effect on the growth variables analyzed, nor did the interactions between factors (detailed results not shown). In contrast, soil moisture was significant in all species, although the variables that differed between moisture levels were different in each case, as detailed below.

In *M. pectinifera*, the only variable that differed between soil moisture treatments was RGR ($F = 6.67$, d.f. = 2,35, $P<0.003$), which was highest in the 60% and lowest in the 5% treatment. An intermediate RGR value was recorded at 25% soil moisture, which did not differ significantly from the RGR values obtained in the other two soil moisture treatments (Table 4).

For *O. denegrii*, to which only the 25% and 60% soil moisture levels were applied, soil moisture had a significant effect in all three growth variables (RGR: $F = 5.66$, d.f. = 1,23, $P = 0.026$; *R*/*S*: $F = 5.25$, d.f. = 1,23, $P = 0.032$; *K*: $F = 30.7$, d.f. = 1,22, $P<0.001$). The highest RGR values were observed in the 60% treatment, while the highest *R*/*S* and *K* values were recorded at 25% soil moisture (Table 4).

Finally, for *C. werdermannii* the effect of soil moisture was significant only for RGR ($F = 32.1$, d.f. = 2,35, $P<0.001$); the lowest value was observed at 5% soil moisture, and values increased with increasing soil moisture, but did not differ significantly (Table 4).

4. Discussion and conclusions

Recalling our first hypothesis, we expected that the seedlings of all three species would have low RGRs and limited plasticity (in terms of changes in biomass allocation patterns) in response to different water and light availability, since the literature suggests that species that have evolved in habitats with limited resources exhibit these type of growth features (Chapin et al., 1993; Grime et al., 1986). However, the RGR values of the species we studied were even lower than those of other species from arid and semi-arid environments (Flores, 2001; Ruedas et al., 2000; Valverde et al., 1997), including other cacti (Flores, 2001; Godínez-Álvarez, 1991; Godínez-Álvarez and Valiente-Banuet, 1998; Miquelajauregui, 2004; Ruedas et al., 2000). It is important to keep in mind that we studied cacti with a globose growth form, while most of those previously studied have a columnar growth form (with the exception of *Mammillaria magnimamma*—Ruedas et al., 2000). This distinction is important because it has been suggested that there is a relationship between RGR and life form (Flores et al., 2004). Our results indicate that this relationship is worthy of further exploration, since it would appear that columnar cacti have higher growth rates than globose cacti. Among globose cacti though, species of *Mammillaria* are relatively fast growing, as indicated by our results for *M. pectinifera* and the results of Ruedas et al. (2000) with *M. magnimamma*. Indeed, the RGR of *M. pectinifera* was an order of magnitude above those of *O. denegrii* and *C. werdermannii*. This coincides with the observations of Martorell and Peters (2005) who have proposed that this species exhibits some semi-ruderal ecological features (i.e., a higher population density in overgrazed ecosystems than in pristine environments), such as a relatively high RGR value.

Regarding plasticity, we expected that it would be narrow in all three species and we hypothesized that, if present, it would be apparent in RGR, rather than in the *R*/*S* ratio (Grime et al., 1986; Nobel, 1988). Our results reveal that plasticity was, in general, rather restricted: it was only observed in some growth variables, and only in response to changes in soil moisture. We expected that the species with the lowest RGR values (i.e., *O. denegrii*) would also be the least plastic; however, it was precisely *O. denegrii* the species with the highest average plasticity (as measured from plasticity indices contrasting the results of the 25% and 60% soil moisture treatments—see Table 5). This was the only species in which significant differences were found between treatments in all the three growth variables; in this species, *K* had the highest plasticity index (Table 5). Regrettably, it was this species for which we did not have enough seedlings to carry out the 5% soil moisture treatment; thus, its degree of plasticity under highly contrasting conditions remains to be investigated.

In contrast to the other two species, *O. denegrii* does not develop a stem with a spiny cover, and it has been classified as "subglobose", because in its adult stage it is more like a rosette formed by triangular tubercules (see Fig. 1). Finally, its roots have been described as fusiform, and are therefore capable of accumulating relatively large amounts of water (Bravo-Hollis and Sánchez-Mejorada, 1991). We believe all these features could account for the relatively greater plasticity in the response of *O. denegrii* compared to those of *C. werdermannii* and *M. pectinifera*. The latter two exhibited a clear plastic response only in relation to their RGR, and the differences in RGR were significant only when the most contrasting treatments were compared (Table 5). In contrast with *O. denegrii*, these two species have a clearly globose growth habit, produce a spiny cover from very early in life and have fibrose roots. Once again a relationship which deserves further attention appears to emerge between growth habit and other morphological features on the one hand, and growth response on the other.

In general, the growth variable with the least plastic response was *R*/*S* ratio (see Table 5). Although there appears to be limited flexibility in the proportional allocation of biomass to roots and shoots (particularly in *M. pectinifera*; see Table 5), the ability of these plants to exploit unpredictable pulses of nutrients and water is thought to reside in their capacity to adjust their RGR in response to varying resource availability. Yet, in *M. pectinifera* and *C. werdermannii* significant variation in RGR was apparent only between the most strongly contrasting conditions (5% vs. 60% soil moisture). This suggests that these species are highly tolerant, i.e., they managed to maintain their RGR values despite a reduction in water availability (from 60% to 25%) without adjusting their *R*/*S* ratio. Again, the response of *O. denegrii* differed from those of the other two. This species did not maintain similar RGR values in the 60% and 25% soil moisture treatments, but did change its *R*/*S* ratio in

Table 5
Plasticity indices for each growth variable and species

	RGR		*R*/*S*		*K*		Average plasticity	
	25% vs. 60%	5% vs. 60%	25% vs. 60%	5% vs. 60%	25% vs. 60%	5% vs. 60%	25% vs. 60%	5% vs. 60%
M. pectinifera	0.32	**0.47**	0.01	0.06	0.20	0.56	0.18	0.36
O. denegrii	**0.25**	n.a.	**0.30**	n.a.	**0.45**	n.a.	0.33	n.a.
C. werdermannii	0.22	**0.77**	0.34	0.08	0.19	0.19	0.25	0.35

Two indices are presented per variable: one calculated by contrasting the 25% and 60% soil moisture treatments (which were done with all three species), and the other calculated by contrasting the most extreme treatments (5% and 60%), which were done with only two species (see note for details on these calculations). Bold figures indicate the two values of the growth variables used for index calculation differed significantly; n.a., no data available.
Note: indices were calculated as the difference between the two values of the variable being contrasted, divided by the highest value of the two (Valladares et al., 2000). Average plasticity is the mean of the three plasticity indices presented in the first three columns.

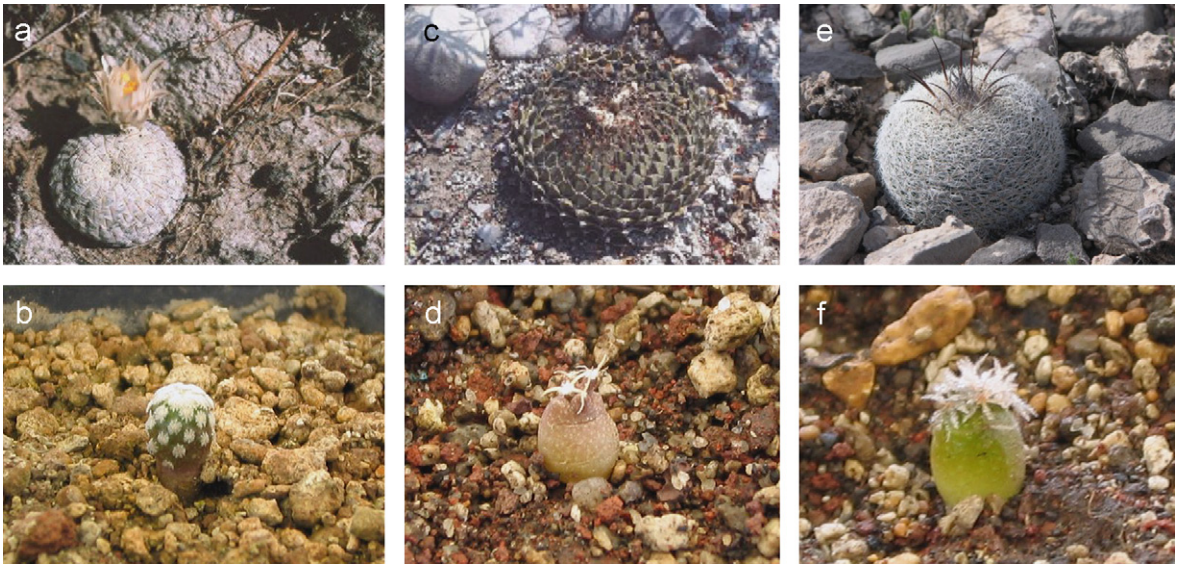

Fig. 1. Photographs of (a) adult *M. pectinifera*, (b) a 6-month-old *M. pectinifera* seedling, (c) adult *O. denegrii*, (d) a 6-month-old *O. denegrii* seedling, (e) adult *C. werdermannii*, and (f) a 6-month-old *C. werdermannii* seedling. The adults were photographed in the field and the seedlings in the greenhouse during the experiments.

response to this reduction in water availability. These results suggest that these species have different ways of facing environmental variation.

For the second hypothesis, we expected that the highest RGR values would occur in the high water availability and high solar radiation treatment; however, as stated in our third hypothesis, we also expected that the growth response of seedlings to moisture would be more dramatic than to radiation. Our results confirmed that the 60% soil moisture treatment resulted in the highest RGR values; however, no differences were observed between radiation levels. The effect of radiation levels on the growth and survival patterns of cactus seedlings has been analyzed by several authors (Flores and Briones, 2001; Flores and Jurado, 1998; Flores et al., 2004; Godínez-Álvarez and Valiente-Banuet, 1998; Mandujano et al., 1998; Miquelajauregui, 2004; Nolasco et al., 1997; Palleiro et al., 2006; Ruedas et al., 2000; Turner et al., 1966; Valiente-Banuet and Ezcurra, 1991), most of whom concluded that a reduction in radiation levels (relative to fully exposed conditions) enhances seedling survival and has a positive effect on RGR. However, our results show that the growth response of the three species studied was unaffected by the different levels of solar radiation. In fact, the RGR values under both conditions were strikingly similar for all three species and no significant differences between radiation treatments were found in the other growth variables analyzed.

It is worth mentioning that the solar radiation levels inside the greenhouse were relatively low compared to those experienced by plants in the field. Even so, there was a strong contrast between the two levels (regardless of the absolute PAR values of the treatments), but this did not result in different RGR values for any of the species. It has been suggested that cacti use the C_3 photosynthetic pathway during their seedling phase (Altesor et al., 1992). In this type of photosynthetic metabolism, light saturation is reached at relatively low PAR levels. Thus, if our seedlings were using the C_3 pathway, it is possible that they reached their light saturation level in both radiation treatments, and this would account for the similarity in the RGR values observed. However, recent studies have shown that some cactus seedlings use the CAM pathway from the very early stages (Hernández-González and Briones-Villareal, 2007). The specific photosynthetic pathway used by seedlings is one aspect of cactus biology that requires further study if establishment patterns in this group are to be better understood.

The response of cactus seedlings to differing moisture levels has seldom been addressed given the difficulty of maintaining constant soil moisture levels under experimental conditions. Most experimental scenarios supplied enough water to guarantee seedling survival, while others reduced solar radiation and thus affected the water levels, thereby confounding the effects of radiation and moisture on cactus growth (Flores et al., 2004; Miquelajauregui, 2004; Nolasco et al., 1997; Ruedas et al., 2000). Given that the presence of a nurse plant both reduces radiation and increases moisture levels, these factors are inextricably linked in nature (Franco and Nobel, 1989; Leirana-Alcocer and Parra-Tabla, 1999; Mandujano et al., 1998; Valiente-Banuet and Ezcurra, 1991). The factorial design of our experiment allowed us to treat these two factors separately. Our results suggest that cactus seedlings are not negatively affected by the reduction in solar radiation levels, but they do benefit greatly from the increased moisture availability under the nurse plant. The high seedling survival observed at these microsites in the field (Jordan and Nobel, 1981; Leirana-Alcocer and Parra-Tabla, 1999; Valiente-Banuet and Ezcurra, 1991) must therefore be related to the increase in RGR resulting from higher water availability.

Note, however, that in our experiment the high water availability treatment (60% soil moisture) represents a condition that might occur only during and shortly after a rainfall event. This high soil moisture may last for longer beneath a nurse plant than in completely exposed conditions (Flores et al., 2004; Franco and Nobel, 1989; Valiente-Banuet and Ezcurra, 1991; Valverde and Zavala-Hurtado, 2006). So, even if plants experience low moisture levels most of the time (perhaps closer to our 5% soil moisture treatment), seedlings established under a nurse plant will benefit from the favorable conditions prevailing after a rainfall event for a longer period of time.

Our findings are also relevant to understanding the way in which ecophysiological traits affect distribution patterns in nature. It has been suggested that early growth and seedling survival patterns are crucial in determining the distribution range of a species (Esparza-Olguín, 2005; Esparza-Olguín et al., 2005). The three species we studied are endemic to small geographical areas, and this may be related to the fact that they show a limited plasticity in their growth traits. Of the three, *M. pectinifera* exhibits the greatest degree of plasticity and also has the widest distribution range (Martorell and Peters, 2005). The relationship between rarity and growth patterns deserves further attention since it will certainly add valuable information to the theory of biological conservation.

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References

Altesor, A., Ezcurra, E., Silva, C., 1992. Changes in the photosynthetic metabolism during the early ontogeny of four cactus species. Acta Oecologia 13, 777–785.

Anderson, E.F., Fitz Maurice, W.A., Fitz Maurice, B., 2002. *Obregonia denegrii*. In: IUCN 2007. IUCN Red List of Threatened Species, www.iucnredlist.org (last accessed 09 June 2008).

Badino, G., Bernabel, T., De Vivo, A., Giulivo, I., Savino, G. (Eds.), 2004. Under the Desert. The Mysterious Waters of Cuatro Ciénegas. Edizioni Tintoreto, Italy.

Bravo-Hollis, H., Sánchez-Mejorada, H., 1991. Las Cactáceas de México, vols. II and III. Universidad Nacional Autónoma de México, Mexico.

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 and Soil 218, 207–214.

Chapin, F.S., Autumn, K., Pugnaire, F., 1993. Evolution of suites of traits in response to environmental stress. American Naturalist 142, S78–S92.

Contreras, C., Valverde, T., 2002. Evaluation of the conservation status of a rare cactus (*Mammillaria crucigera*) through the analysis of its population dynamics. Journal of Arid Environments 51, 89–102.

Esparza-Olguín, L.G., 2005. Estudio comparativo de tres especies de cactáceas columnares del género *Neobuxbaumia* que difieren en su nivel de rareza: un enfoque genético-demográfico. Doctoral Thesis, Facultad de Ciencias, Universidad Nacional Autónoma de México.

Esparza-Olguín, L., Valverde, T., Vilchis-Anaya, E., 2002. Demographic analysis of a rare columnar cactus (*Neobuxbaumia macrocephala*) in the Tehuacán Valley, México. Biological Conservation 103, 349–359.

Esparza-Olguín, L., Valverde, T., Mandujano, M.C., 2005. Comparative demographic analysis of three *Neobuxbaumia* species (Cactaceae) with differing degree of rarity. Population Ecology 47, 229–245.

Evans, G.C., 1972. The Quantitative Analysis of Plant Growth. Blackwell, Oxford.

Flores, J.D., 2001. Dinámica del establecimiento de plantas de diferentes formas de vida del desierto de Tehuacán, México. Doctoral Thesis, Instituto de Ecología, A.C. Xalapa, Veracruz, Mexico.

Flores, J., Briones, O., 2001. Plant life form and germination in a Mexican inter tropical desert: effects of soil water potential and temperature. Journal of Arid Environments 47, 485–497.

Flores, J., Jurado, E., 1998. Germination and early growth traits of 14 plant species native to northern Mexico. Southwestern Naturalist 43, 40–46.

Flores, J., Briones, O., Flores, A., Sánchez-Colón, S., 2004. Effect of predation and solar exposure on the emergence and survival of desert seedlings of contrasting life-forms. Journal of Arid Environments 58, 1–18.

Flores-Martínez, A., Ezcurra, E., Sánchez-Colón, S., 1994. Effect of *Neobuxbaumia tetetzo* on growth and fecundity of its nurse plant *Mimosa luisana*. Journal of Ecology 82, 325–330.

Franco, A.C., Nobel, P.S., 1989. Effect of nurse plants on the microhabitat and growth of cacti. Journal of Ecology 77, 870–886.

Gibson, A.C., Nobel, P.S., 1986. The Cactus Primer. Harvard University Press, USA.

Godínez-Álvarez, H.O., 1991. Propagación de cactáceas por semilla: una experiencia para su cultivo y conservación. Bachelor of Science Thesis, Facultad de Ciencias, Universidad Nacional Autónoma de México.

Godínez-Álvarez, H., Valiente-Banuet, A., 1998. Germination and early seedling growth of Tehuacan Valley cacti species: the role of soils and seed ingestion by dispersers on seedling growth. Journal of Arid Environments 39, 21–31.

Godínez-Álvarez, H.O., Valverde, T., Ortega Baes, P., 2003. Demographic trends in the Cactaceae. The Botanical Review 69, 173–203.

Grime, J.P., 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. The American Naturalist 111, 1169–1194.

Grime, J.P., Crick, J.C., Rincon, E., 1986. The ecological significance of plasticity. In: Jennings, D.H., Trewawas, A.J. (Eds.), Plasticity in Plants. Company of Biologists, Cambridge, UK.

Hernández-González, O., Briones-Villareal, O., 2007. Crassulacean acid metabolism photosynthesis in columnar cactus seedlings during ontogeny: the effect of light on nocturnal acidity accumulation and chlorophyll fluorescence. American Journal of Botany 94, 1344–1351.

Hunt, D., 1992. CITES Cactaceae Checklist. Royal Botanic Gardens Kew, UK.

Jordan, P., Nobel, P.S., 1981. Seedling establishment of *Ferocactus acanthodes* in relation to drought. Ecology 62, 901–906.

Lambers, H., Poorter, H., 1992. Inherent Variation in Growth Rate Between Higher Plants: A Search for Physiological Causes and Ecological Consequences. Advances in Ecological Research, vol. 23. Academic Press Limited, USA.
Leirana-Alcocer, J., Parra-Tabla, V., 1999. Factors affecting the distribution, abundance and seedling survival of *Mammillaria gaumeri*, an endemic cactus of coastal Yucatán, México. Journal of Arid Environments 41, 421–428.
Mandujano, M.C., Montaña, C., Méndez, I., Golubov, J., 1998. The relative contributions of sexual reproduction and clonal propagation in *Opuntia rastrera* from two habitats in the Chihuahuan Desert. Journal of Ecology 86, 911–921.
Martínez, J.G., Suzán, H., Alcázar, A., 1994. Aspectos ecológicos y demográficos de *Neolloydia pseudopectinata* (Backeberg) E.F. Anderson. Cactáceas y Suculentas Mexicanas 39, 27–33.
Martorell, C., Peters, E., 2005. The measurement of chronic disturbance and its effects on the threatened cactus *Mammillaria pectinifera*. Conservation Biology 124 (22), 199–207.
Miquelajauregui, Y., 2004. Estudio comparativo de la sobrevivencia y el crecimiento temprano de dos especies de *Neobuxbaumia* (Cactaceae) que difieren en su nivel de rareza. Bachelor of Science Thesis, Facultad de Ciencias, Universidad Nacional Autónoma de México.
Nobel, P.S., 1988. Environmental Biology of Agaves and Cacti. Cambridge University Press, UK.
Nolasco, H., Vega-Villasante, F., Diaz-Rondero, A., 1997. Seed germination of *Stenocereus thurberi* (Cactaceae) under different solar radiation levels. Journal of Arid Environments 36, 123–132.
Norma Oficial Mexicana, NOM-059-ECOL-2001. Protección ambiental-especies nativas de México de Flora y Fauna Silvestres-Categorías de riesgo y especificaciones para su inclusión, exclusión o cambio-Lista de especies en riesgo. SEMARNAT. D.O.F. 03-06-2002.
Palleiro, N., Mandujano, M.C., Golubov, J., 2006. Aborted fruits of *Opuntia microdasys* (Cactaceae): insurance against reproductive failure. American Journal of Botany 93, 505–511.
Rodríguez-Ortega, C.E., Ezcurra, E., 2000. Distribución espacial en el hábitat de *Mammillaria pectinifera* y *M. carnea* en el valle de Zapotitlán Salinas, Puebla, México. Cactáceas y Suculentas Mexicanas 45, 4–14.
Ruedas, M., Valverde, T., Castillo, S., 2000. Respuesta germinativa y crecimiento de plántulas de *Mammillaria magnimamma* (Cactaceae) bajo diferentes condiciones ambientales. Boletín de la Sociedad Botánica de México 66, 25–35.
Steenbergh, W.F., Lowe, C.H., 1969. Critical factors during the first years of life of the Saguaro (*Cereus giganteus*) at Saguaro National Monument, Arizona. Ecology 50, 825–834.
Taiz, L., Zeiger, E., 2002. Plant Physiology. Sinauer Associates, Inc., USA.
Turner, R., Stanley, M., Alcorn, M., Olin, G., Booth, J.A., 1966. The influence of shade, soil, and water on Saguaro seedling establishment. Botanical Gazette 127, 95–102.
Valiente-Banuet, A., Ezcurra, E., 1991. Shade as a cause of the association between the cactus *Neobuxbaumia tetetzo* and the nurse shrub *Mimosa luisana* in the Tehuacán Valley, México. Journal of Ecology 79, 961–971.
Valladares, F., Wright, S.J., Lasso, E., Kitajima, K., Pearcy, R., 2000. Plastic phenotypic response to light of 16 congeneric shrubs from a Panamanian rainforest. Ecology 81, 1925–1936.
Valverde, P.L., Zavala-Hurtado, J.A., 2006. Assessing the ecological status of *Mammillaria pectinifera* Weber (Cactaceae), a rare and threatened species endemic of the Tehuacan-Cuicatlán Region in Central Mexico. Journal of Arid Environments 64, 193–208.
Valverde, T., Pisanty, I., Rincón, E., 1997. Growth response of six tropical dune plant species to different nutrient regimes. Journal of Coastal Research 13, 497–505.
Zavala-Hurtado, J.A., Valverde, P.L., 2003. Habitat restriction in *Mammillaria pectinifera*, a threatened endemic Mexican cactus. Journal of Vegetation Science 14, 891–898.