The relative importance of solar radiation and soil origin in cactus seedling survivorship at two spatial scales: Plant association and microhabitat

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The relative importance of solar radiation and soil origin in cactus seedling survivorship at two spatial scales: plant association and microhabitat

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Abstract

Question: What is the relative importance of solar radiation intensity and soil origin for cactus establishment at the spatial scales of microhabitat and plant association?

Location: Tehuacán-Cuicatlán region, central Mexico.

Methods: The seedling survivorship of *Myrtillocactus geometrizans, Neobuxbaumia tetetzo* and *Opuntia pilifera* was assessed. A garden experiment was conducted involving two light treatments (direct solar radiation and artificial shade) for seedlings growing in soil from different microhabitats (under the canopy of a *Parkinsonia praecox* nurse plant and in an open area) from three plant associations (*tetechera, sotolinera* and *mezquitera*) in a semi-arid inter-tropical ecosystem. It was predicted that seedling survival would be higher: (1) under the artificial shade treatment; (2) in soil from the microhabitat under the canopy of the nurse tree; (3) in soil from the plant association with the highest concentrations of carbon (C), nitrogen (N) and phosphorus (P); and (iv) in the species with the largest seed mass.

Results: Seedlings of the three species survived better in the shade. Despite the fact that soil taken under nurse plants has a higher concentration of nutrients than that from open areas, seedling survivorship did not differ between these microhabitats. *Opuntia pilifera*, the species with higher seed mass, survived better than *M. geometrizans* and *N. tetetzo*, whose seedling survival did not differ. Seedling survivorship differed between soils taken from the different plant associations. Higher survival rates were observed in soil from plant associations with the lowest concentration of total and available P (i.e. *sotolinera* and *tetechera*) but with a high concentration of C, total N, nitrate and ammonium.

Conclusions: The relative importance of shade and soil origin on seedling survivorship depends on the spatial scale. At the microhabitat level, shade is crucial for seedling establishment, whereas soil type is not. However, soil seems important at the plant association scale. An adaptation to the most common habitat of the Zapotitlán Valley, where soil has high quantities of Ca (as carbonate), little available P but relatively high available N, could explain the better early cactus seedling survivorship in the *tetechera* and *sotolinera*.

Introduction

Vegetation in arid and semi-arid zones is strongly influenced by abiotic components such as temperature and humidity. Evidence of this is the differential survivorship of seedlings under shade trees and bushes (Shreve 1931; Turner et al. 1966; Franco & Nobel 1989; Flores & Jurado 2003) or other objects (Munguía-Rosas & Sosa 2008), as opposed to open areas. In arid zones, temperature buffering and reduction in moisture loss produced by the shade of any object is the abiotic component of the 'nurse effect' (see Flores & Jurado 2003). The biotic component of the

nurse effect includes all biological processes influencing soil nutrient spatial and temporal availability (and the ways in which nutrients are lost from the soil) and, particularly, the microbial activity involved in the processes of making essential nutrients available to plants. Areas under tree canopies and bushes where such nutrients abound are known as fertility islands or resource islands (Reynolds et al. 1999). Along with a high concentration of organic matter and nitrogen (N), such microhabitats serve as feeding, nesting and perching sites for various animals (Sosa & Fleming 2002; Suzán & Sosa 2006). Besides the nurse effect, other biotic interactions such as seed dispersal and predation may influence the establishment and survivorship of seedlings under canopies.

Survivorship or growth under shade/direct sunlight treatments has been reported for cactus seedlings in the biogeographical region of Tehuacán-Cuicatlán. For example, the seedlings of *Neobuxbaumia tetetzo*, *Pachycereus holli-anus* (Valiente-Banuet & Ezcurra 1991; Godínez-Álvarez & Valiente-Banuet 1998) and *Wilcoxia viperina* (Álvarez & Montaña 1997) were more successful in shade conditions, whereas *Cephalocereus chrysacanthus* and *Stenocereus stellatus* (Álvarez & Montaña 1997) had greater survivorship in direct solar radiation conditions. A neutral effect was reported for *Ferocactus latispinus* (Álvarez & Montaña 1997).

Using different soil types, Godínez-Álvarez & Valiente-Banuet (1998) observed better performance for *P. holli-anus* seedlings in soils with a higher content of organic matter and N. However, by working with soil taken from beneath *Mimosa luisana* and adjacent bare areas (with less organic matter but similar N content), Álvarez & Montaña (1997) found cases of higher seedling survivorship (*Stenocereus stellatus*) in soil taken from beneath nurse trees as well as in soil from bare areas (*Ferocactus latispinus* and *Wilcoxia viperina*), and cases of similar survivorship in both soil types (*Cephalocereus chrysacanthus*). Working with non-cactus species, Franco-Pizaña et al. (1996) found that both *Celtis pallida* and *Acacia smallii* seedlings exhibited increased growth in soil with more nutritious resources (from areas under nurse plants) than in soil with fewer resources (from bare areas) in direct solar radiation but not in a shade treatment. In addition to extrinsic factors, cactus establishment and survivorship may depend on intrinsic factors such as seed size and resistance to pathogens (Fritz & Simms 1992). In general, large-seeded plant species show higher survivorship after germination than small-seeded species, supposedly due to a higher supply of seed reserves (Lloret et al. 1999; Leishman et al. 2000; Moles & Westoby 2004).

Efforts to understand cactus seedling survivorship have focused on the microhabitat scale, especially on compari-sons between open sites (poor soil and direct solar radiation) and under the canopy of nurse plants (relatively rich soil and less intense solar radiation) within the same plant associations. To date, little is known about the effect of soils on cactus seedling survivorship at a scale larger than microhabitat, for example at the plant association or landscape unit scale. Soils in the main microhabitats of arid environments, under plant cover and in bare ground, may be affected differentially through plant associations due to different litter composition, root exudates, mineral composition of the substrate or animal droppings, among other factors.

These ideas were explored in the three larger plant associations (*mezquitera*, *sotolinera* and *tetechera*) of a subtropical semi-arid region of central Mexico (Tehuacán-Cuicatlán Valley). The three larger cacti (*Myrtillocactus geometrizans*, *Neobuxbaumia tetetzo* and *Opuntia pilifera*) and the most common nurse (*Parkinsonia praecox*; Perroni-Ventura et al. 2006) shared by the three plant associations were selected. The aim of this study was to evaluate the seedling survival of these three cacti that differ in growth form and seed size. Specifically, we endeavoured to identify the possible facilitating role of fertility islands under the same nurse species in different plant associations. For this purpose, we conducted a common garden experiment involving seedling establishment under two light conditions (reduced solar radiation, RS, and direct solar radiation, DSR) and in soil from two microhabitats (under the nurse plant *P. praecox* and open areas) from the three mentioned plant associations. There are two advantages to this experimental strategy. On the one hand, it isolates the effect of shade (lower temperature, solar radiation and evapotranspiration) under a nurse plant from the effect of differences in soil nutrients triggered by litterfall quality and quantity (fertility island). On the other, it allows separation of the mid-term effect of nutrients contributed by litter from the nurse plant currently living on the site from the long-term effect due to the geoform, bedrock (and its derived mineral soil) and the residual effect of other nurse plants – even of different species – that have occupied the site throughout the years. Such long-term effect can be assessed in soils from bare areas, whereas the mid-term effect is observed in soil under nurse plants. In addition, we analysed pH and basic nutrient content to compare fertility of soils from the six origins.

Our predictions were as follows: seedling survivorship would be higher (1) under the shade treatment than under direct solar radiation; (2) in soil taken from under a *P. praecox* canopy, due to the higher concentration of nutrients found in these microhabitats than in open spaces; (3) in soil from the plant association that had the highest concentration of nutrients (C, N and P); and (4) in the species with the largest seed mass.

Methods

Study site

Zapotitlán Valley (18°20′ N, 97°28′ W, 1500 m a.s.l.) is on the outskirts of the town of Zapotitlán Salinas, Puebla, Mexico. Its annual mean rainfall is 381 mm and the mean temperature is 21 °C (Montaña & Valiente-Banuet 1998 and references therein). The rainy season is from April– May to September–October, with very little inter-annual seasonal variability. Soils in Zapotitlán Salinas Valley are derived from calcareous sedimentary rocks of marine origin and metamorphic rocks, and have a high concentration of carbonates and an alkaline pH. Vegetation corresponds to semi-arid scrubland (Rzedowski 1978). Within the valley, there are three main plant associations (Zavala 1982): *mezquitera*, *sotolinera* and *tetechera*. *Tetechera* is dominated by the columnar cactus *Neobuxbaumia tetetzo*, which may be accompanied by *Mimosa luisana*, *Aeschynomene compacta*, *Cordia cylindrostachya*, *Mammillaria colina*, *Ruellia* sp., *Eysenhardtia polystachia* and *Opuntia pilifera*. A thin layer of soil overlies a rocky substrate. *Sotolinera* is dominated by *Beaucarnea gracilis* plus *Yucca periculosa*, *Myrtillocactus geometrizans*, *Pachycereus hollianus*, *Opuntia pilifera* and *Agave kerchovei*. It lies on a rolling terrain with a gravelly soil of clayey texture. *Prosopis laevigata* dominates the *mezquitera*, and *Parkinsonia praecox*, *Myrtillocactus geometrizans*, *Stenocereus pruinosus*, *S. stellatus* and *Pachycereus hollianus* may also be common species. *Mezquitera* has higher cover than *tetechera* and *sotolinera*, and it also has the higher cover and abundance of *M. geometrizans* and *O. pilifera*. It is on flat terrain on the bottom of the valley, with a 3–5 cm sandy soil layer developed on deep alluvial sediments (Zavala 1982; see Table 1 for more details on soil characteristics). Soils of the *sotolinera* and *tetechera* were developed from *in situ* primary bedrock, whereas soils of the *mezquitera* were developed from transported alluvial material. Distance between study sites of the three plant associations varies between 3 and 4 km. All seeds and soils used in the experiment were collected in these three sites.

Study species

Myrtillocactus geometrizans (C. Martius) Console is a columnar cactus with abundant branches that can reach 6 m in height. It blooms from February to early March. Fruiting begins in mid-March and runs through September, reaching its peak in May and June (R. Palacios-Silva, unpublished data). *Neobuxbaumia tetetzo* (F.A.C. Weber) Backeb. is one of the largest columnar cacti in the region, reaching up to 15 m (Bravo-Hollis 1978). It blooms between April and May and fruiting takes place from late May to early June. *Opuntia pilifera* (F.A.C. Weber) is a prickly pear cac-

tus that can reach 3 m in height; it blooms from March to June. Fruiting takes place from June to August, peaking in July. *Myrtillocactus geometrizans* and *N. tetetzo* seeds are 0.053 ± 0.001 mm^3 ($n = 83$) and 0.105 ± 0.002 mm^3 ($n = 170$) in volume (volumes estimated using the formula of circular cones), respectively, and that of *O. pilifera* is 18.81 ± 0.489 mm^3 ($n = 105$, volume estimated using the formula of a squat cylinder). There are *Opuntia pilifera* and *Myrtillocactus geometrizans* in the three plant associations, while *N. tetetzo* is found in the *tetechera* only. *Opuntia pilifera* is commonest in *tetechera*, then in *sotolinera* and *mezquitera*; by contrast, the sequence for *M. geometrizans* is *tetechera*, *mezquitera* and *sotolinera*.

Soil collection and analyses

Soils of the under nurse plant microhabitat were collected under the canopy of *Parkinsonia praecox* (Ruíz & Pavón) Hawkins, Caesalpinaceae. *Parkinsonia praecox* is a dominant legume tree in Zapotitlán Salinas Valley (Zavala 1982), which forms fertility islands (Perroni-Ventura et al. 2006). This species is distributed mainly along arid and semi-arid regions in the western part of the United States and Mexico (MacMahon & Wagner 1985), Bolivia and Argentina.

The soil samples used for analyses of soil fertility were collected from the valley's three main plant associations: *mezquitera* (sampling area of ca. 3 ha), *sotolinera* (ca. 4 ha) and *tetechera* (ca. 7 ha). In each plant association, soil was taken from two microhabitats: the area under *P. praecox* canopy and in bare areas nearby. Soil collection was done at the end of the 2010 rainy season, in late September. Six *P. praecox* individuals of at least 3 m canopy diameter and at least 2 m height were randomly selected from each plant association. Under the canopy of each shrub (after removing litter), a 500-g sample was taken at a depth of 0– 10 cm and a distance of 70 cm from the trunk, with a randomly determined azimuth. In the bare area further than 4 m from the canopy border of each tree, a 500-g soil sample was collected (after removing litter) at a location determined randomly, care being taken to ensure that there was no vertical projection of canopies within a 4-m radius. Collected soil was stored during 15 d in black bags and kept in a dry, fresh place for analysis. The minimum distance between plant associations sampled was 3 km.

The following parameters were measured for each soil sample: pH, inorganic C, organic C, total N, ammonium, nitrate, total P and available P (orthophosphate). Additionally, the following ratios were assessed: organic C:total N, total N:total P, total N:(ammonium + nitrate) and total P: available P. Organic C concentration was calculated as the difference between the concentrations of total C and inorganic C. To measure total C and inorganic C, we used a CO_2 automatic analyser (UIC Mod. CM5012). Total N and

Table 1. Characteristics of the three main plant associations in Zapotitlán Salinas Valley in Central Mexico.

Plant association*	Altitude (m a.s.l.)	Geoform according to García-Oliva (1991)	Soil according to López-Galindo et al. (2003)	Physical characteristics of soil		
			Type	Depth	Rockiness	Texture
Mezquitera	1490	Alluvial terrace and mountain lower slopes. Bedrock: Cretacic lutites and sandstones	Fluvisol and Calcaric Regosol	Deep	Low	Loam and Clay-Loam
Sotolinera	1550	Mountain lower slopes. Bedrock: Cretacic lutites and sandstones	Calcacic Feozem	Shallow	Medium	Loam
Tetechera	1500	Mountain lower slopes. Bedrock: Cretacic lutites and sandstone. Paleozoic limestones	Calcacic Feozem	Shallow	High	Sandy-Loam and Clay-Loam

*Dominant species, whose common names mesquite (*Prosopis laevigata*), sotolín (*Beaucarnea gracilis*) and tetecho (*Neobuxbaumia tetetzo*) give the name to the plant associations.

total P were determined on a Braun+Luebbe 3 Autoanalyzer (Norderstedt, Germany) after acid digestion; N with a modified Kjeldahl method (Technicon Industrial Systems 1977); and P using the molybdate colorimetric method after ascorbic acid reduction (Murphy & Riley 1962). Ammonium and nitrate were determined using the method of Binkley & Hart (1989) and on a Braun+Luebbe 3 Autoanalyzer. Available P (water soluble) was determined in the same autoanalyser, as orthophosphate. The pH was measured in a 1:2 soil:water extract.

Soil samples to be used in the survival experiment were taken from the same sites (and with same procedure) where soil samples for soil fertility analyses were taken. Moreover, soil samples collected for the survival experiment were mixed in six pooled soil samples (one for each combination of plant association and microhabitat). The ten pots assigned to each of the six experimental combinations of plant association and microhabitat were filled with these pooled soil samples in order to minimize microsite and plant association internal soil heterogeneity.

Seed collection and seedling production

Mature *M. geometrizans*, *N. tetetzo* and *O. pilifera* fruits were collected immediately after abscission. The seeds were washed to eliminate mucilage, air dried and stored in paper bags at room temperature. A total of 1800 seeds (three species × three plant associations × two microhabitats × two light conditions × ten cylindrical plastic pots [repetitions, 9.5-cm high × 7.4-cm diameter] × 5 seeds per pot) were used to obtain the seedlings needed for the experiment. Plastic pots were kept in a non-shaded nursery and watered daily to field capacity in the evening. After 30 d, all but the largest seedling in each pot were removed. Pots with one seedling each were the experimental units.

Garden experiment design

In order to ensure the safety of the experiment, it was carried out on privately owned land under natural environmental conditions in the city of Tehuacán, Puebla, México, 18 km NNE of Zapotitlán Salinas. Mean annual temperature is 18.04 °C and mean annual precipitation is 383.21 mm. The rainy season in Tehuacán runs from May to October, with a peak between June and September. All climatic data are from CONAGUA (2010) for the period 1964–2010.

The experiment was designed to test for three factors potentially related to seedling survivorship: solar radiation (direct or artificial shade), soil from two microhabitats (under *P. praecox* canopy or from bare areas) and soil from different plant associations (*mezquitera*, *sotolinera* or

tetechera). A fourth factor, plant species (*M. geometrizans*, *N. tetetzo* and *O. pilifera*) was also included in the model. The experiment had a fixed-effects factorial design with ten replicates per treatment combination. One hundred and twenty experimental units were used for each cactus species (a total of 360 units in the whole experiment). After pot thinning, half of the 20 pots of each species × plant association × microhabitat combination were randomly assigned to shade treatment, and the other half to direct solar radiation treatment. These 60 randomly located pots were individually covered with a black plastic mesh shade that reduced incident radiation by 50% (RS treatment). Photosynthetically active radiation (PAR) received in each shade (RS) and direct solar radiation (DSR) condition was 846.14 ± 59.75 µmol·m^{-2}·s^{-1} ($n = 9$) and 1694.4 ± 119.03 µmol·m^{-2}·s^{-1}, $n = 9$, respectively. PAR was measured with a radiometer (Li-1000; Li-Cor, Lincoln, NE, US) at noon on a sunny day in June. Thus, ten replicates of each combination of treatments were mixed randomly on a 1.20-m height bench. Pots assigned to the direct solar radiation treatment did not have any kind of cover. All pots were watered to field capacity at the beginning and every other day in the evening. Seedling survival was recorded daily for the first 15 d, every other day for the third and fourth weeks, weekly during the following month and every 2 wks until the experiment ended. The experiment started on 16 June 2011 (i.e. 30 d after the seeds were planted in the pots) and ended on 16 June 2012.

Statistical analysis

Soil differences among plant associations

Soil in bare areas is the result of interaction between the mineral composition of the substrate and the vegetation–soil relationships developed at the site over time. This relationship integrates the temporal succession of activities of the different plants that developed at a particular site over the years. In contrast, soil under the nurse plant represents the biological interaction between the soil of that particular plant association and the current activity of the nurse plant (production of litter, roots and exudates; microclimatic changes, etc.). It would therefore be worthwhile to do a separate analysis of the effect of plant association soils in bare areas and under nurse plants. The former would show differences due to plant associations, while the latter would reveal the effects of the biological interaction between the nurse plant and plant association soil. Thus, plant association differences for each soil parameter (pH, inorganic C, organic C, total N, ammonium, nitrate, total P and available P) were analysed separately for each microhabitat (bare areas and under nurse plants) through one-way ANOVAs followed by Tukey multiple comparisons. Non-parametric rank transformations were applied to non-normally distributed variables according to Conover & Iman (1981).

Soil differences among microhabitats

To compare soil parameters measured in the two microhabitats, two-way ANOVAs with two fixed-effects factors were carried out (plant association with three levels and microhabitat with two) for each soil variable. Inclusion of the plant association factor in this analysis allowed evaluation of the statistical interaction between microhabitat and plant association. In this analysis, plant association mean values are calculated by averaging the values of both microhabitats (see the previous section) and their comparison is of no value for the purposes of this study.

Differences in seedling survivorship

We recorded survivorship of each seedling in days up until the experiment ended after 1 yr. Failure time data as a dependent variable should be explored with survival analysis because these data do not meet the assumptions of normality and equal variance of data (thus identical shape of the failure time distributions) of classical ANOVA approaches. In addition, classical ANOVA cannot account for censored data (see Pyke & Thompson 1986; Fox 2001; Crawley 2007). Because we were interested in comparing the survival curves among treatments that are thought to affect survivorship multiplicatively, we fitted an accelerated failure time regression model. Survival data over 1 yr were taken as right-censored, which permits proper comparison of survival curves (Pyke & Thompson 1986). We assessed best fit under the four most common survival distributions using the Akaike information criterion (AIC; Crawley 2007): (1) the exponential distribution, which is characterized by a constant failure rate; (2) the Weibull distribution, characterized by a continuous increase or decrease in failure rates (Pyke & Thompson 1986); (3) the log-normal; and (4) the log-logistic distributions, which are characterized by failure rates that initially increase to a maximum and then decrease (Fox 2001). The statistical model included solar radiation (shade or direct solar radiation), seedling species (*M. geometrizans*, *N. tetetzo* or *O. pilifera*), plant association as a soil source (*mezquitera*, *sotolinera* or *tetechera*) and microhabitat fertility (under *P. praecox* or bare area), and all possible interactions as factors. All analyses were performed using the R statistical package version 2.12.2 (R Foundation for Statistical Computing, Vienna, AT) and the Survival package (http://CRAN. R-project.org/package=survival). In every case, the value of α was 0.05.

Results

Soil nutrients

Differences between plant associations

One-way ANOVAs (Appendix S1) showed that more soil variables differed between plant associations under the canopies of *P. praecox* than in bare areas (Table 2). Biological activity under canopies is expressed as differences in pH, inorganic C, total P, available P and the ratios total N: total P and total N:(ammonium + nitrate) (Table 2). In bare areas only inorganic C, nitrate, available P and the ratio total N:(ammonium + nitrate) differed (Table 2).

Differences between microhabitats

The two-way ANOVAs (Appendix S2) showed that there were differences between microhabitat in pH, organic C, total N and the ratio organic C:total N, and that there was a significant interaction of plant association × microhabitat in nitrate, and the ratios total N:total P and total N:(ammonium + nitrate). Organic C, total N and total C:total N were higher under *P. praecox* canopy, whereas pH was higher in bare areas (Fig. 1). The statistical interactions showed that nitrate and the ratio total N:total P tended to be higher under *P. praecox*, but this was significant only in the *mezquitera* for nitrate and in the *tetechera* for the ratio total N:total P. In contrast, the ratio total N:(ammonium + nitrate) tended to be higher in bare areas, but this was significant only in the *mezquitera* (Fig. 2).

Seedling survivorship

Survival data were best described with a log-logistic distribution. The highest mortality for all three species was recorded before 50 d, and from then onwards mortality rates decreased. Shade treatment, cactus species and plant association had significant effects on seedling survivorship, while microhabitat had no such effect (Table 3). Both a triple interaction (cactus species × plant association × microhabitat) and the four-fold interaction of all main factors were also significant (Table 3). Seedling survivorship was higher under artificial shade than when exposed to direct solar radiation (Fig. 3a). Regarding cactus species, survivorship of *O. pilifera* seedlings was higher than that of *M. geometrizans* or *N. tetetzo* (Fig. 3b). Seedling survival was lower in soils from the *mezquitera* than in soils from the remaining two plant associations (Fig. 3c), and did not differ between microhabitats (Fig. 3d).

Discussion

The results show that, at the microhabitat scale, the survivorship of *O. pilifera*, *M. geometrizans* and *N. tetetzo* seedlings depends more on the intensity of solar radiation than on soil fertility. At the plant association scale, soil seems to play a more important role for the survivorship of all cactus species.

Corroborating the first hypothesis, the experiment showed that the shade treatment had a positive effect on the three cacti seedling survivorship. The effect of shade on cactus seedling survivorship is not always positive (Nobel 1988; Álvarez & Montaña 1997; Flores-Torres & Montaña 2012), although it is for many species (Shreve 1931; Turner et al. 1966; Nobel 1988; Valiente-Banuet & Ezcurra 1991; Álvarez & Montaña 1997; Godínez-Álvarez & Valiente-Banuet 1998; Carrillo-García et al. 2000b). Seedling survivorship for other *Opuntia* species, such as *O. rastrera* and *O. microdasys* in the Chihuahuan Desert (Mandujano

Table 2. Mean ± SE of soil variables in two microhabitas (bare area and under nurse plant) from three plant associations (*mezquitera, sotolinera* and *tetechera*) from the Tehuacan Valley.

Soil variables	Bare area			Nurse		
	Mezquitera	*Sotolinera*	*Tetechera*	*Mezquitera*	*Sotolinera*	*Tetechera*
pH	8.6 ± 0.1 (a)	8.6 ± 0.07 (a)	8.6 ± 0.08 (a)	8.2 ± 0.07 (a)	8.4 ± 0.07 (a,b)	8.7 ± 0.17 (b)
Inorganic C (mg·g^{-1})	9.1 ± 1.6 (a)	35.0 ± 0.9 (c)	28.0 ± 2.0 (b)	7.5 ± 1.5 (a)	35.4 ± 0.6 (b)	34.6 ± 7.7 (b)
Organic C (mg·g^{-1})	20.6 ± 4.8 (a)	13.3 ± 1.5 (a)	15.9 ± 2.5 (a)	29.9 ± 3.6 (a)	24.4 ± 2.1 (a)	29.3 ± 6.1 (a)
Total N (mg·g^{-1})	2.2 ± 0.4 (a)	1.6 ± 0.2 (a)	1.9 ± 0.1 (a)	2.8 ± 0.3 (a)	2.4 ± 0.1 (a)	2.8 ± 0.3 (a)
Total P (mg·g^{-1})	0.41 ± 0.05 (a)	0.25 ± 0.02 (a)	0.36 ± 0.06 (a)	0.44 ± 0.05 (b)	0.37 ± 0.08 (a,b)	0.25 ± 0.03 (a)
Ammonium (µg·g^{-1})	0.96 ± 0.1 (a)	0.97 ± 0.2 (a)	1.52 ± 0.3 (a)	1.11 ± 0.2 (a)	1.12 ± 0.2 (a)	1.49 ± 0.3 (a)
Nitrate (µg·g^{-1})	4.6 ± 0.8 (a,b)	3.5 ± 0.3 (a)	6.7 ± 1.0 (b)	14.2 ± 1.9 (a)	8.6 ± 0.5 (a)	10.7 ± 2.2 (a)
Available P (µg·g^{-1})	1.6 ± 0.3 (b)	0.7 ± 0.2 (a)	1.0 ± 0.04 (a,b)	2.6 ± 0.6 (b)	0.97 ± 0.1 (a)	0.99 ± 0.2 (a)
Organic C:Total N	8.7 ± 0.8 (a)	8.7 ± 1.2 (a)	8.1 ± 0.7 (a)	10.9 ± 0.6 (a)	10.1 ± 0.6 (a)	9.9 ± 1.3 (a)
Total N: Ammonium + Nitrate	404 ± 35 (b)	376 ± 51 (a,b)	248 ± 33 (a)	187 ± 17 (a)	248 ± 4 (b)	246 ± 27 (b)
Total N:Total P	5.5 ± 0.5 (a)	6.5 ± 0.7 (a)	5.8 ± 0.7 (a)	6.4 ± 0.65 (a)	7.4 ± 1.0 (a,b)	12.6 ± 2.2 (b)
Total P:Available P	310 ± 68 (a)	482 ± 138 (a)	351 ± 68 (a)	262 ± 101 (a)	507 ± 219 (a)	330 ± 90 (a)

Different letters inside each microhabitat indicate significant (Tukey-test, $P < 0.05$) between-plant association differences in the measured soil variable, after a one-way ANOVA. In all cases $n = 6$.
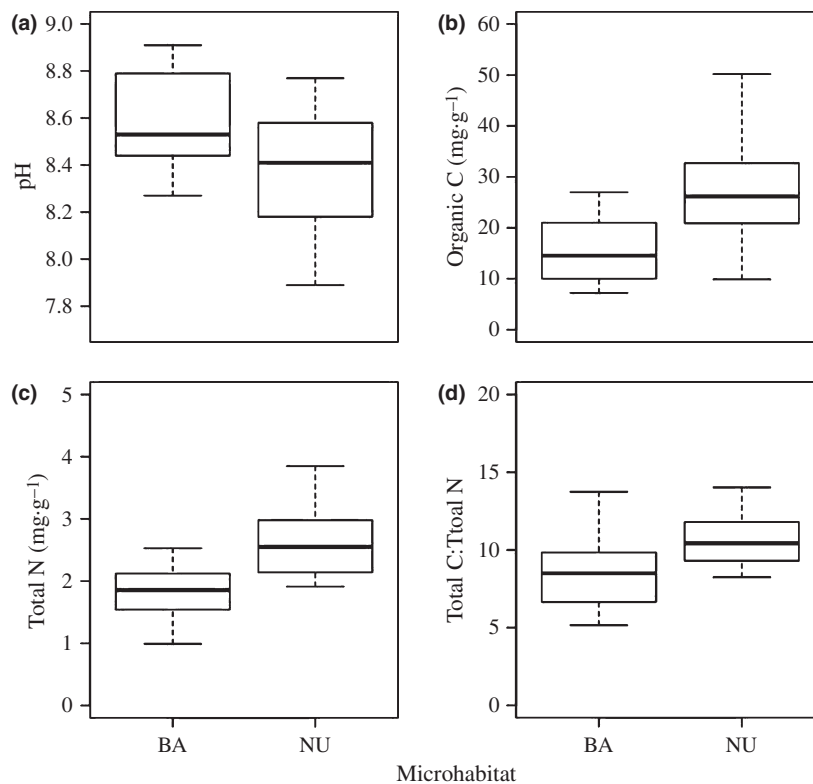
Fig. 1. Box and whisker plots showing the median (heavy line inside boxes), upper and lower quartiles (boxes) and 1.5 times the interquartile range (whiskers) of soil parameters that showed statistical differences ($P < 0.05$) between their mean values in two microhabitats (BA = bare areas; NU = nurse) according to a two-way ANOVA. Pooled values from three plant associations (*Mezquitera*, *Sotolinera* and *Tetechera*) from the Zapotitlán Salinas Valley of Central Mexico are shown.

et al. 1998; Palleiro et al. 2006), can also exhibit a positive response to increased shade. For *M. geometrizans*, little data exist. However, for other species of the same life form, such as those of the genus *Stenocereus*, it has been reported that soil moisture is more important than solar radiation (Ayala-Cordero et al. 2006). Although the relative importance of hydric stress and solar radiation on *M. geometrizans* seedling survivorship is not known, Hernández-González & Briones (2007) suggest that this species may be sensitive to photoinhibition. That would explain its low survivorship rates as compared to *O. pilifera* (Fig. 3b). Bravo-Mendoza et al. (2007) found that *N. tetetzo* seedling establishment in the same area is higher under its nurse plant, where the incident PAR is 80%. The resistance of *N. tetetzo* to withstand PAR over 50% may explain its high survivorship compared to *M. geometrizans* (Fig. 3b).

It must be mentioned that in other extreme ecosystems it is not the attenuation of solar radiation that is the main factor facilitating plant establishment as in hot deserts. In cold deserts and alpine environments (with very low winter temperatures and low water availability due to climatic or physiological drought), protection against extreme low

temperatures and cold dry winds could be the most important factors for seedling survivorship (Richardson & Friedland 2009). Marr (1977) and Soriano et al. (1994) reported positive effects for seedling establishment arising from the protection given by plants against direct and indirect effects of strong winds in ecosystems with very cold winters. At any rate, any plant or object that, through physical protection, facilitates seedlings to resist these unfavourable conditions, will function as a nurse plant or object.

Our second hypothesis was not supported: the experiment showed no improvement in *O. pilifera*, *M. geometrizans* and *N. tetetzo* seedling survivorship associated with soil taken from beneath the nurse plant as compared to soil from bare areas. As in the present study, most research reports higher nutrient concentrations under nurse plants than in nearby bare areas (Table 4); mentioning that seedling establishment may benefit from the higher nutrient conditions present in soil under nurse canopies (Flores & Jurado 2003). However, our results suggest that for *O. pilifera*, *M. geometrizans* and *N. tetetzo* seedling survivorship does not depend on nutrient content generated by biologi-
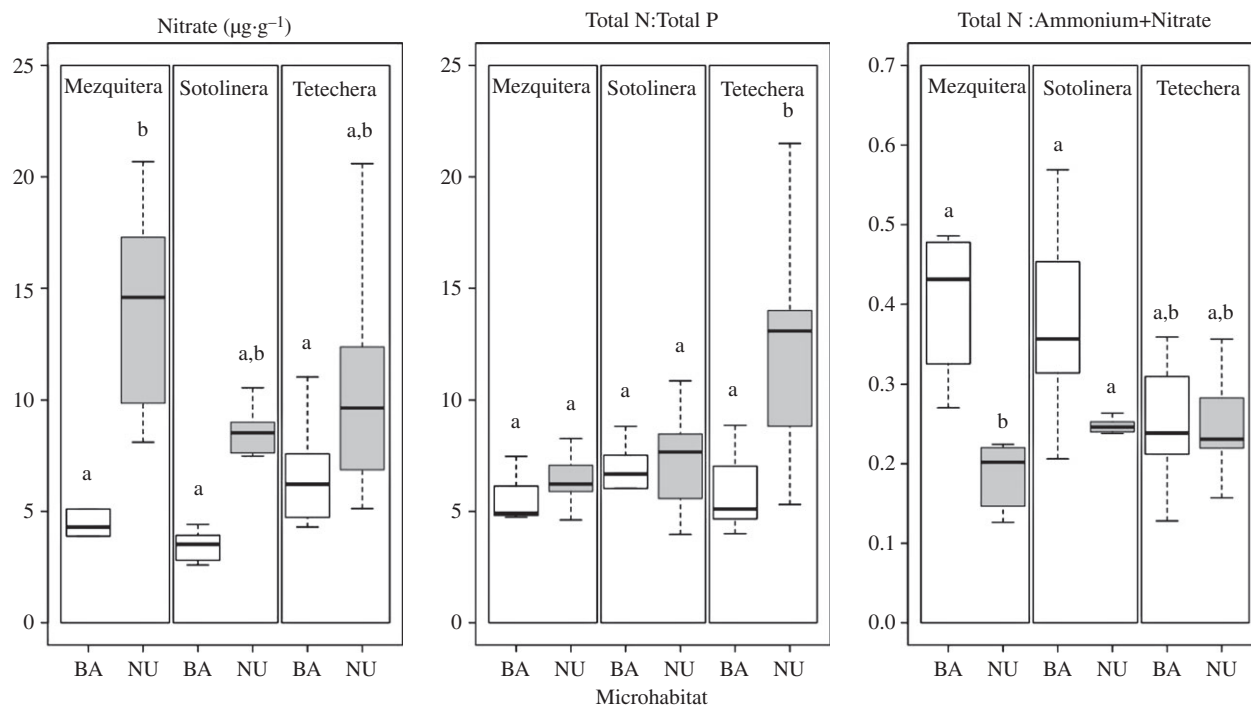
Fig. 2. Box and whisker plots showing the median (heavy line inside boxes), upper and lower quartiles (boxes) and 1.5 times the interquartile range (whiskers) of soil parameters that showed a significant interaction ($P < 0.05$) between microhabitats (BA = bare areas, N = nurse) and plant associations (*Mezquitera*, *Sotolinera*, *Tetechera*) according to a two-way ANOVA. Different letters above boxes indicate statistical difference between means ($P < 0.05$).

Table 3. Analyses of deviance of the effect of four factors on the time to death of cactus seedlings from the Zapotitlán Valley in central Mexico. Factors are: solar radiation condition (DSR, direct solar radiation; RS, 50% PAR reduction), seedling species (*Myrtillocactus geometrizans*, *Neobuxbaumia tetetzo* and *Opuntia pilifera*), soil from plant association (*mezquitera*, *sotolinera*, *tetechera*), and soil from microhabitat (bare areas and under *P. praecox* canopies). Deviance is the contribution to the maximized likelihood function. See Methods (*Statistical analysis. Differences in seedling survivorship*) for details of the statistical model.

Source	df	Deviance (χ^2)	P
Solar radiation (R)	1	54.27	<0.0001
Species (S)	2	10.98	0.0041
Plant association (Pa)	2	7.68	0.021
Microhabitat (M)	1	0.06	0.799
R × S	2	5.58	0.061
R × Pa	2	5.65	0.059
S × Pa	4	1.32	0.859
R × M	1	0.01	0.919
S × M	2	0.26	0.878
Pa × M	2	1.07	0.586
R × S × Pa	4	7.38	0.117
R × S × M	2	0.78	0.676
R × Pa × M	2	0.42	0.810
S × Pa × M	4	11.7	0.019
R × S × Pa × M	4	13.87	0.0077
Error	323	2492.84	
Total	358	2613.96	

cal activity under nurse canopies. This was also observed for the non-cactus species *Celtis pallida* and *Acacia smalli*: in shade conditions, seedling performance did not vary in accordance with the soil microhabitat of origin (Franco-Pizaña et al. 1996). The authors attributed the protégé–nurse association to factors other than soil nutrition, such as seed dispersers, soil moisture and solar radiation. Such factors could also be related to the higher seedling survivorship of *M. geometrizans*, *N. tetetzo* and *O. pilifera* under nurse plants.

Our results agree with the results found in most North American hot deserts, i.e. that at the microhabitat scale the attenuation of solar radiation is the key factor allowing the establishment of cactus species (particularly columnar or candelabra-like cacti; Shreve 1931; Turner et al. 1966; Nobel 1988; Valiente-Banuet & Ezcurra 1991; Álvarez & Montaña 1997; Godínez-Álvarez & Valiente-Banuet 1998; Carrillo-García et al. 2000b). Soil-linked factors (e.g. fertility, humidity, texture, etc.) are likely to have greater relevance in more advanced stages of the plant life cycle, where the presence of a more developed root system is evident (Pavón & Briones 2000).

However, it is interesting that organic C and total N, two soil parameters closely related to soil fertility, differed between microhabitats (Appendix S2). Also, pH
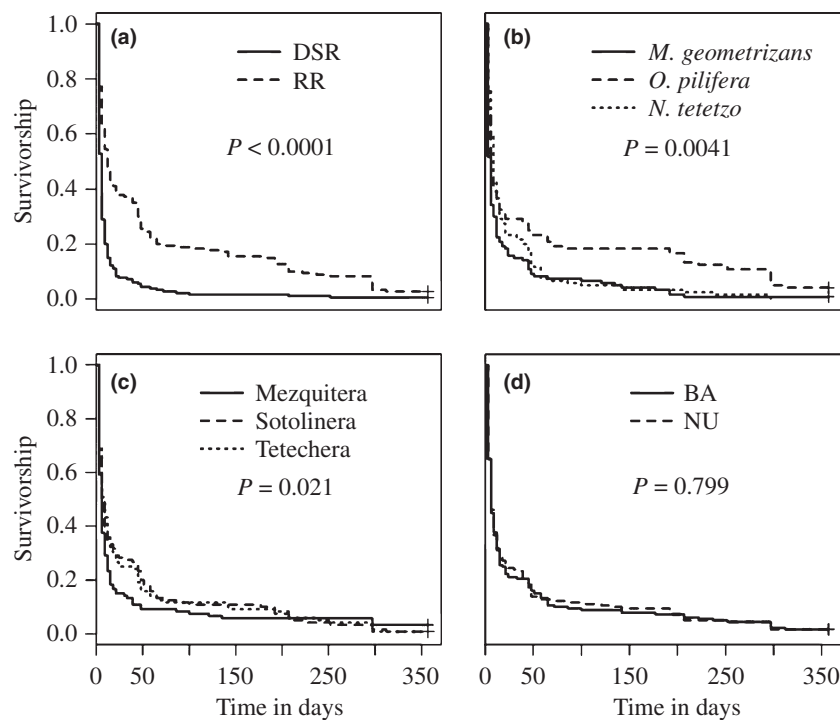
Fig. 3. Seedling survivorship for (**a**) solar radiation conditions (DSR, direct solar radiation; RS, 50% PAR reduction); (**b**) seedling species; (**c**) plant association; and (**d**) soil from different microhabitats (bare area = BA and under nurse canopy = NU). *P*-value in each plot is the probability that seedling survivorship curves differ between treatments (see Table 3).

Table 4. Mean ± SE of soil N concentration under the canopy of nurse species and in open spaces in different arid and semi-arid regions of North America.

Species	Under nurse plants	In open spaces	References
Cercidium microphylum[†]	0.37 ± 0.05 mg·g^{-1}	0.14 ± 0.01 mg·g^{-1}	Franco & Nobel (1989)
Hilaria rigida[†]	0.46 ± 0.03 mg·g^{-1}	0.29 ± 0.04 mg·g^{-1}	Franco & Nobel (1989)
Ambrosia deltoidea[†]	0.35 ± 0.001 mg·g^{-1}	0.14 ± 0.001 mg·g^{-1}	Franco & Nobel (1989)
Mimosa luisana[‡]	0.22 ± 0.02 mg·g^{-1}*	0.19 ± 0.01 mg·g^{-1}*	Valiente-Banuet et al. (1991)
Prosopis glandulosa[§]	1.40 ± 0.1 g·kg^{-1}	0.53 ± 0.04 g·kg^{-1}	Franco-Pizaña et al. (1996)
Mimosa luisana[‡]	1.70 ± 0.03 mg·g^{-1}	1.20 ± 0.01 mg·g^{-1}	Álvarez & Montaña (1997)
Prosopis articulata[†]	0.07 mg·g^{-1}	0.02 mg·g^{-1}	Bashan et al. (2000)
P. articulata[†]	0.34 mg·g^{-1}	0.24 mg·g^{-1}	Carrillo-García et al. (2000a)
Olneya tesota[†]	0.30 mg·g^{-1}	0.25 mg·g^{-1}	Carrillo-García et al. 2000b;
Artemisia tridentata[§]	5.79 ± 0.63 µg·g^{-1}	5.22 ± 1.05 µg·g^{-1}	Forseth et al. (2001)
Chrysothamnus nauseosus[§]			
Parkinsonia praecox[‡]	1.90 ± 0.1 mg·g^{-1}	1.20 ± 0.1 mg·g^{-1}	Perroni-Ventura et al. (2006)
P. laevigata[‡]	2.90 ± 0.1 mg·g^{-1}	1.20 ± 0.1 mg·g^{-1}	Perroni-Ventura et al. (2006)
P. praecox[‡]	2.65 ± 0.132 mg·g^{-1}	1.92 ± 0.14 mg·g^{-1}	Present study

[†]Sonoran Desert.
[‡]Zapotitlán Salinas.
[§]Chihuahuan Desert.
*No statistical differences, *P* > 0.05.

and inorganic C concentration differed between plant association, suggesting that organic and inorganic C and total N content of fertility islands may have different dynamics at the plant association level: both nurse plant (through variation in the capacity to shed leaf litter and attracting vertebrates, whose droppings or pellets contribute organic waste) and soil (through variation in the capacity to retain nutrients and maintain microbiota)

contribute differentially to soil fertility in each plant association.

For *M. geometrizans*, *N. tetetzo* and *O. pilifera*, the differences in incident solar radiation are more important than differences in soil nutrient content at the level of microhabitat. The importance of reduced solar radiation may be due to the cactus' lack of capacity to cope with desiccation (Nobel & Bobich 2002) or to the immaturity of the crassulacean acid metabolism (CAM) photosynthetic system during early seedling stages (Loza-Cornejo et al. 2003; Ayala-Cordero et al. 2006; but see Hernández-González & Briones 2007). Nevertheless, soil may play other vital roles in later cactus development; although in this study its importance for seedling establishment is observed only at the plant association level.

The relationship between the soil component and cactus seedling survivorship at the plant association level had not been previously explored. In our study, analyses revealed that only inorganic C, nitrate and available P concentration differed among soils from bare areas of the three plant associations; the lowest available P concentration corresponding to *sotolinera*. By contrast, most nutrients differed in amount in soils under the nurse plants of all three plant associations (including total and available P, which was lower in *sotolinera* and *tetechera*). The experiment showed an effect of plant association soil on cactus seedling survivorship: seedlings growing on soils from the *sotolinera* and the *tetechera* had higher survivorship up to 200 d of age. Thereafter, their survival was very similar to that of *mezquitera* (which is the plant association with the highest soil fertility). The better survival during the first 200 d in *sotolinera* and *tetechera* is hard to explain, given that both plant associations did not have the highest N and P concentrations. A likely explanation is that the combination of a high concentration of inorganic C (Ca in carbonate form) and nitrate, and a low concentration of available P in the soil of the *sotolinera* and *tetechera* account for increased seedling survival. It has been reported that the total N:total P quotient is key to promoting the mechanisms that help a recently emerged seedling to become fixed in the soil, as well as facilitating the mycorrhizal association that allows seedlings to acquire nutrients directly from the soil during the period of true root formation (Paul & Clark 1996). Carrillo-García et al. (1999, 2000b) showed higher survivorship rate in seedlings of the columnar cactus *Pachycereus pringlei* that are inoculated with mycorrhizae, as compared to those that are not. Both P and Ca are important in energy and metabolic reactions of plants, for growth in the case of P, and for the regulation of diverse processes such as photosynthesis, oxidative cell division, immune system, homeostasis and activation of enzymes in the case of Ca in plants (Fraústo da Silva & Williams 2001). Although soil fertility

may be an influential factor in the survival of cactus seedlings at the plant association level, given the experimental design used in this work, it is not possible to demonstrate which soil fertility parameters are the decisive factors. Other factors not discussed herein, related to the soil, such as moisture and microbial activity may also be influencing the phenomenon.

Taylor et al. (1990) and Schamp et al. (2002) hypothesize that most plant species adapt better to wide distribution areas or to environments that have been more common over the geological history of the planet than to less common or more recent ones. The same authors mention that the most common habitats and those with the widest distribution characteristically have intermediate or low levels of soil fertility. Those that are too poor or too rich in nutrients are rare; thus, it takes a long time for substantial numbers of species to adapt to them. The superior performance of seedlings at the *sotolinera* and *tetechera* may correspond to the history of adaptation to the most common habitat in Zapotitlán Salinas Valley.

On the other hand, the effect of the geologic origin of the plant association soils cannot be ignored. It must be noted that the main difference between soils of *sotolinera* and *tetechera*, as compared to *mezquitera*, is inorganic C content (Table 2), which is due to differences in calcium carbonate content. It must be remembered that soils of the *sotolinera* and *tetechera* are developed from *in situ* primary calcareous bedrock, whereas soils of the *mezquitera* are developed from transported alluvial materials with a lower calcium content due to the mixture of calcareous as well as of metamorphic rocks that are common in the higher portions of the watersheds (García-Oliva 2001; López-Galindo et al. 2003). But soil calcium plays a much more complex role than simply that of a nutrient such as N or P; it also regulates soil chemical and physical properties (Bronick & Lal 2005), it fixes P but often promotes N availability in acid conditions (Van Raij 1991), it helps to reduce high sodium content and regulates salinity in the soil (Alva et al. 1991), but may also pose a problem for plants in regulating its absorption in excess conditions (Fraústo da Silva & Williams 2001). Studied cacti have evolved in calcic soils and, like many other succulents, they can use their large vacuoles to get rid of excess calcium, and might also profit from the 'good' properties of calcic soils. Cacti are well adapted to soils with a high calcium content (Nobel 1988).

As expected, *O. pilifera* survivorship was higher than for *M. geometrizans* and *N. tetetzo*. A possible explanation may be that *O. pilifera* seeds and seedlings are larger than those of *M. geometrizans* and *N. tetetzo*. It is likely that larger seedlings are better able to face adverse conditions in their first dry season, according to two non-mutually exclusive hypotheses: larger reserves in their cotyledons (Moles &

Westoby 2004) or a larger allocation to root production (Lloret et al. 1999). We can conclude that, without taking herbivory into consideration, seedling survivorship for these three cactus species is determined mainly by the amount of solar radiation to which they are exposed. By contrast, differences in soil nutrient content among microhabitats are not reflected in better seedling survivorship for either species. However, it is reported for the first time that differential cactus survivorship is related to plant association soil characteristics. Elements in soil (nitrate, available P and Ca) may contribute to substantial initial improvement in seedling survivorship in the *sotolinera* and *tetechera*, the plant associations with a more calcareous soil. By contrast, differences in soil nutrient content among microhabitats are not reflected in better seedling survivorship for either species.

Acknowledgements

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Table of one-way Anova of each soil parameter on three plant associations (*mezquitera, sotolinera and tetechera*).

Appendixs S2. Two-way Anova for each soil variable.