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## Comparative performance of the giant cardon cactus (*Pachycereus pringlei*) seedlings under two leguminous nurse plant species

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### Abstract

Recruitment and survival of cacti in North American deserts are facilitated under the canopy of nurse plants. In the Sonoran desert, the giant cardon cactus (*Pachycereus pringlei*) is associated with ironwood (*Olneya tesota*) and mesquite (*Prosopis glandulosa*) trees. We hypothesized that *P. pringlei* seedlings would perform better under ironwood than mesquite, on the basis of the mature individuals patterns of association. In Bahia Kino, Sonora, we conducted a field experiment from 1992 to 2000 comparing the performance of *P. pringlei* seedlings under randomly selected *O. tesota*, and *P. glandulosa* trees. Results indicated that *P. pringlei* seedlings under *P. glandulosa* had significantly higher survival and were significantly taller than those under *O. tesota* after 8 years. Micro-environment and soil properties beneath both trees did not differ significantly, while tree physiognomies differed only in height at the base of the canopy and basal area. As a deciduous tree, *P. glandulosa* provided more litter to the ground than *O. tesota*. These results therefore did not support our initial hypothesis. We discuss how other biotic factors such as differential seed dispersal might explain why *P. pringlei* establishment is more strongly spatially associated with *O. tesota*.

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**Keywords:** Cardon; Columnar cacti; Facilitation; Ironwood; Mesquite; Nurse plants

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## 1. Introduction

In arid ecosystems, the shade provided by perennial longer-lived plants, creates rich diversity islands that play a fundamental role in the vegetation dynamics (Búrquez et al., 1999). In the Sonoran Desert, recruitment and survival of many cacti occurs primarily under the canopy of perennial plants (Suzán et al., 1994; Callaway, 1995; Tielbörger and Kadmon, 2000), which buffers the microenvironment beneath their canopies from extreme heat and freezes (Turner et al., 1966; McAuliffe, 1988; Parker, 1988), increasing water infiltration and nutrient availability (Felker and Clark, 1981), and/or conferring concealment against seed and seedling predation (McAuliffe, 1984).

There is evidence that the shade provided by nurse plants enhances survival rates of their protégés (Patten, 1978; Valiente-Banuet and Ezcurra, 1991). Therefore, the life stages more likely to be influenced by nurse plants are the seed and seedling stages (Jordan and Nobel, 1981; Cody, 1993). In the Sonoran Desert, complete shading from direct sunlight decreases the maximum soil surface temperature by 11 °C on a summer day, and raises the minimum temperature by 3 °C on a winter day (Franco and Nobel, 1989). Thermal analysis of columnar cacti showed considerable differences in plant temperatures inside versus outside the canopy of shrubs (Nobel, 1980).

In addition, tree canopies function as foci of plant recruitment in arid habitats where trees are spatially isolated within large extensions of bare ground or grass (Archer et al., 1988; Kellman and Kading, 1992; McClanahan and Wolfe, 1993). Isolated trees attract birds and bats which seek roosting and nesting substrates and many of them disperse seeds beneath the canopy by defecating, or by dropping regurgitated seeds to feed their chicks (Dean et al., 1990; Milton et al., 1998; Tewksbury et al., 1999; Galindo-González et al., 2000).

Association patterns suggest that some perennials are disproportionately colonized as nurse plants (Suzán et al., 1996). Among the factors that may determine the quality of perennials as nurse plants are: (1) crown architecture, which affects light extinction coefficients, photosynthetic active radiation (PAR), and temperature buffering (Suzán et al., 1997); (2) litter contribution to the upper layers of soil, which affects nutrient contents and availability to associated and nurse plants and conspicuousness of seeds and seedlings to predators (Sosa and Fleming, 2002); and (3) the presence of arbuscular–mycorrhizal fungi and nitrogen-fixing bacteria in soils beneath perennial plants (Carrillo-García et al., 1999).

In the southern regions of the Sonoran Desert, two arborescent legumes are extremely important nurse trees: *Olneya tesota* (ironwood), and *Prosopis glandulosa* (mesquite). *O. tesota* is a small (up to 6 m tall) semi-deciduous wash (ephemeral streams) facultative tree, that loses leaves completely only during periods of extreme freezes or droughts (Suzán et al., 1997), and that have many plant species spatially associated with its canopies (West et al., 2000). In contrast, *P. glandulosa* is a dominant species restricted to washes and xeroriparian streams (Búrquez and Quintana, 1994), whose stems may branch from the base into two to four trunks, and with crowns up to 5 m tall and 10 m wide. This species sheds its leaves from January

to March. Both trees are used for roosting or nesting by birds which have few other tall trees to rely on.

An important columnar cactus in the southern regions of the Sonoran Desert is *Pachycereus pringlei* (the giant cardon cactus), one of the tallest cacti in the world that contributes importantly in basal area and biomass to desert plant communities (Sosa, 1997). *P. pringlei* is a trioecious species, pollinated mainly by bats (Fleming et al., 1994). Its seeds are dispersed by birds and less frequently by mammals, by ants and by a single lizard species (Sosa, 1997). In the Central Gulf Coast subdivision of the Sonoran Desert, *P. pringlei* is partially associated with several perennials, particularly *O. tesota* (Suzán et al., 1996) and *P. glandulosa* (Carrillo-García et al., 1999). The recruitment of *P. pringlei* seedlings is restricted to microenvironments buffered by these two tree legumes canopies. Germination and seedling survival are dramatically higher beneath leguminous nurses than in open spaces when predators are excluded (Sosa, 1997).

The relative importance of the roles of these two nurse species has not been addressed for any columnar cactus. In the Gulf Coast subdivision of the Sonoran desert *O. tesota* appears to be the main nurse for *P. pringlei* seedlings (Sosa and Fleming, 2002). Therefore, we hypothesize that seedling growth and survival would be higher beneath *O. tesota* than beneath *P. glandulosa*. In order to test this hypothesis, we designed a field experiment with the following objectives:

- (a) to measure the survival and growth of a seedling cohort split beneath *O. tesota* and *P. glandulosa* trees;
- (b) to analyse the microenvironmental conditions beneath the two nurse species (soil temperature, stem temperature, PAR, and canopy cover) and their relation to cardon seedling performance;
- (c) to analyse the possible effects of soil and litter conditions beneath the nurse plant canopies on the *P. pringlei* seedlings; and
- (d) to prove differential seed dispersal favoring ironwood microhabitats.

## 2. Materials and methods

### 2.1. Study site

The experiment was conducted in Rancho San Germán (28°55' N, 111°54' W), north of the Bahía Kino port (municipality of Hermosillo, Sonora, Mexico). The vegetation of the area is a xeric-shrubland, dominated in xeroriparian streams by *P. glandulosa*, *O. tesota* and *P. pringlei*. This area of the Gulf Coast has undergone intense exploitation of ironwood (for carving wood) and mesquite (for charcoal) since 1960. However, since the beginning of the experiment in 1992 there has been a hiatus in the cutting of both tree species at the study site by carvers and charcoal makers.

## 2.2. Seedling survival and growth

To test the hypothesis of differential survivorship of cardon seedlings beneath the canopies of *O. tesota* and *P. glandulosa*, we transplanted *P. pringlei* seedlings to soil under the canopies of each nurse tree species and recorded survival and growth during each of 8 years. Previous studies conducted in 1990–1991 at the same study site indicated no survival at all in open spaces (Sosa, 1997).

We extracted seeds from 24 fruits collected from six *P. pringlei* individuals in the study area in May 1992. More than 360 seeds were placed on moist filter paper in Petri dishes and kept at room temperature (30 °C) in Bahia Kino. Seed germination percentages were higher than 90%, and we used only seedlings that sprouted between 3 and 10 days after sowing. To avoid damage to root hairs and reduce stress when transplanting, we prepared (25 cm × 25 cm × 2.54 cm) blocks of soil gleaned from the ground surface taken below the experimental trees, and put into cardboard molds. Two weeks after the seedlings had sprouted, 10 healthy seedlings were randomly selected and transplanted into each soil block. Seedlings that did not survive the transplanting (less than 3%) were replaced. When seedlings were 1 month old and still had their cotyledons, we took the blocks and placed them in the field under the canopies of *O. tesota* and *P. glandulosa* trees. After watering each block gently to assure uniform moisture conditions, we slipped the block into two excavated molds, each one set at 0.5 m from the main stem in random directions. We then placed the seedlings and covered them with chickenwire cages (25 cm × 25 cm × 20 cm) to reduce seedling predation.

Once seedlings were in the field, we did not water them. The experimental design was a nested experiment (Montgomery, 1976) with a fixed main factor (two tree species: *O. tesota* and *P. glandulosa*), six randomly chosen trees nested per species, and two mesh-wired plots nested within each tree. The seedlings were mapped within each box, and the height and diameter of each seedling were measured with millimeter calipers. Bi-annual measurements of survival and growth (diameter, height) were collected between 1992 and 1994 and annual measurements were recorded between 1998 and 2000.

We analysed the survival of the seedlings with the Kaplan-Meier method with right-censored data, adjusted by the Weibull plot, and tested statistical differences among the survival curves of seedlings beneath *O. tesota* and *P. glandulosa* with the Log-Rank and Wilcoxon tests. The height and diameter dynamics of the seedlings were analysed by a multi-variate analysis of variance with repeated measures (MANOVA) for the original nested design. We obtained also the growth index suggested by Malda et al. (1999; growth index = height × diameter<sup>2</sup>), and analysed differences by a repeated measures procedure (fixed effects). We ran all statistical analyses with the JMP software (JMP, 1995).

## 2.3. Microenvironmental conditions

We measured soils and meristematic stem extreme temperatures in a randomly selected summer day, June 25, 1993, around 14.00 h, and in a randomly selected

winter day, December 7, 1993, around 7.00 h. We recorded soil surface temperatures for the north and south projected shade beneath the canopies of the experimental trees, and in nearby non-shaded spaces, using omega thermocouples connected to a LICOR 1000 data-logger. The seedling stem temperatures were measured also with omega thermocouples. Finally on the same days we recorded the PAR with a LICOR PAR sensor connected to the LICOR 1000 data logger by a measurement of photosynthetic flux density in  $\mu\text{mol m}^{-2} \text{s}^{-1}$ .

#### 2.4. Canopy conditions

We randomly selected typical mature trees of comparable sizes for both nurse species, and measured in 1993 and 2000 for each experimental tree the height (m), height to the base of the canopy (m), canopy radius (m) in four directions, and diameter (transformed into basal area) of main stems 30 cm over ground. We also recorded leaf area indices (LAI) in July 16, 2000 with a LICOR LAI 2000 instrument, considering the main stem of each tree as the central point. Measurements (four inside the canopy and one outside) were taken during sunrise (0500–0530 h). The coefficient of light diffusion and standard errors for the LAIs were calculated by the LAI 2000 data-logger. Analyses included a MANOVA for physiognomic features and an ANOVA for LAIs.

#### 2.5. Soil conditions

To determine the pH and available nutrients, we collected 12 soil samples in June 2000, one under each *P. glandulosa* and *O. tesota* experimental tree canopies. Each sample consisted of three randomly selected subsamples of the first 3 cm of a profile from the surface that were blended in a plastic bag. We did not collect soil from open spaces because previous studies determined that open spaces at this study site present lower nutrient concentrations than under *P. glandulosa* canopies (Sosa, 1997). We analysed soil samples for: pH, organic matter, nitrogen percentages, available phosphorus, and Na, K, Ca, and Mg contents by standard methods (Jackson, 1976). We analysed differences by a one way MANOVA.

We indirectly estimated leaf litter production, using the wired cages protecting seedlings as traps. For this purpose, we opened the ceiling of the cages in the last year of measurements, and measured depth of accumulated litter in the four corners of the cage with a caliper, obtaining an average height of the column of accumulated litter. We used a nested design with four measurements per tree (cage).

#### 2.6. Seed dispersal beneath canopies

We indirectly measured seed dispersal beneath *P. glandulosa* and *O. tesota* nurse trees through estimation of relative abundance of bird nests of known avian dispersers on nurse canopies, under the assumption that abundance of nests are positively correlated with the probability of dropping viable seeds under canopies (Olin et al., 1989). To evaluate whether the canopies of both nurse species were

differentially chosen for nesting by cardon bird dispersers, we counted nests of *P. pringlei* known bird dispersers and sampled canopy cover of the main nurse plants of cardon in the study area. We then compared the observed proportion of each tree species chosen for nesting with the expected proportion according to the relative cover of each nurse species in 0.2 ha (Sosa, 1997). This comparison was made with a goodness of fit test. In 1990, we counted all nurse species (any perennial with *P. pringlei* growing beneath its canopy) in two 10 × 100 m plots. Canopy cover was estimated as a circle with the maximum canopy radius. Because the number of nests built on nurse species was too small in the plots used to sample canopy cover, in June 1993, we counted all nests of dispersers built in trees or shrubs in a polygonal area of approximately 2 ha, along the transition between the lower and upper bajada.

### 3. Results

#### 3.1. Seedling survival and growth

Seedlings transplanted to the experimental area in 1992 showed contrasting survival behavior beneath the two nurse plant species (Fig. 1). In the earliest stages after transplanting, survival rates were high for both species until the first year, then mortality increased differentially among those seedlings beneath both nurses intensifying in the last 2 (drought) years. Eight years after transplanting (2900 days

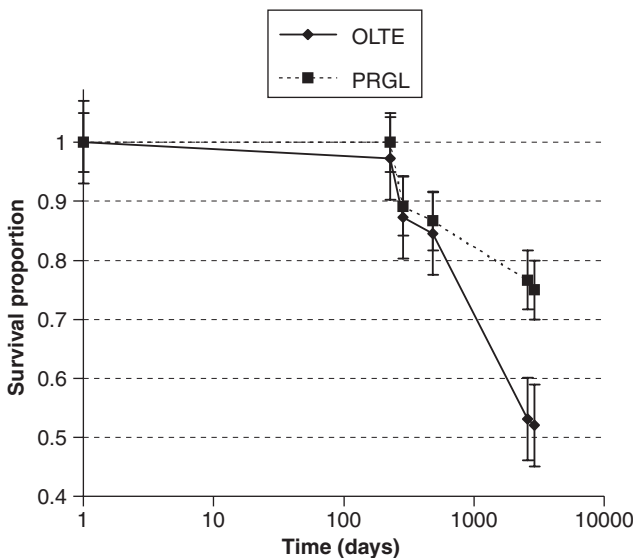


Fig. 1. Seedling survival beneath two nurse plant species (OLTE = *Oleña tesota*; PRGL = *Prosopis glandulosa*). Notice that X-axis is  $\log_{10}$  scaled. Kaplan-Meier Weibull method indicates significant survival differences with the Log-Rank test:  $\chi^2_1 = 11.3940$ ,  $p = 0.0007$ ; and with the Wilcoxon test:  $\chi^2_1 = 10.0769$ ,  $p = 0.0015$ .

Fig. 1) a significantly higher number of carbon seedlings survived beneath *P. glandulosa* canopies than beneath *O. tesota* canopies.

The differential effects detected in seedling survival were also detected in height growth in the 8 years study period. At the end of the experiment, a MANOVA test that included height and diameter, indicated significant differences between the two nurse species. At time of transplanting, seedlings under both nurse species showed no differences in height ( $t_{238} = -1.422$ ,  $p = 0.16$ ) or diameter ( $t_{238} = -0.777$ ,  $p = 0.94$ ), but at the end of the experiment seedlings under *P. glandulosa* were significantly taller ( $mean = 99.58$ ,  $se = 4.3$ ), than under *O. tesota* ( $mean = 86.26$ ,  $se = 5.4$ ) as indicated by the MANOVA analysis (Wilks  $\lambda = 0.97$ ,  $F_{1,142} = 4.09$ ,  $p = 0.024$ ). The height difference was reflected in a marginal difference in the growth index between the two nurse species according to the repeated measures MANOVA analysis (Wilks  $\lambda = 0.97$ ,  $F_{1,120} = 3.7035$ ,  $p = .0567$ )

### 3.2. Microenvironmental conditions

Maximum soil surface temperatures ( $mean \pm se$ ) of a summer day were  $44.77^{\circ}\text{C} \pm 1.062$ ,  $47.98^{\circ}\text{C} \pm 1.16$ , and  $59.11^{\circ}\text{C} \pm 1.078$ , beneath ironwood shade, mesquite shade and in open space, respectively. On the other hand, soil temperatures at 07:00 h on a winter day were  $18.84^{\circ}\text{C} \pm 0.36$ ,  $17.84^{\circ}\text{C} \pm 1.17$ , and  $17.72^{\circ}\text{C} \pm 0.37$  in ironwood shade, mesquite shade and open space, respectively. Soil temperatures were significantly higher only in open spaces in summer than under nurse plants, as predicted by the nurse plant hypothesis ( $F_{2,37} = 46.5$ ,  $p < 0.0001$ ). However, soil temperatures under canopies did not differ between species in summer or in wintertime. Consequently, meristematic stem temperature of seedlings showed similar values between nurse species in both summer ( $F_{1,18} = 2.55$ ,  $p = 0.61$ ), and winter records ( $F_{1,22} = 0.703$ ,  $p = 0.41$ ).

As expected, PAR during the day was higher in open spaces, than under nurse plants canopies along the day (Fig. 2). Significant differences were detected at the three times examined, 07:00, 14:00, and 17:00 h ( $F_{2,37} = 29.51$ ,  $F_{2,37} = 102.36$ , and  $F_{2,37} = 21.73$ , respectively;  $p < 0.0001$  for all cases). However, both nurse plants showed no difference in PAR measurements over the length of a day; either in summer ( $t_{18} = 0.36$ ,  $p = 0.72$ ) or winter ( $t_{22} = 0.28$ ,  $p = 0.78$ ).

### 3.3. Canopy conditions

A multi-variate ANOVA found overall differences of architecture features between both tree species (Wilks'  $\lambda = 0.197$ ,  $F_{5,6} = 4.90$ ,  $p = 0.04$ ). *O. tesota* had larger individuals with significantly higher basal area ( $684 \pm 74.2 \text{ cm}^2$ ;  $F_{1,10} = 4.83$ ,  $p = 0.05$ ) and the base of the canopy at a higher height ( $1.03 \pm 0.18 \text{ m}$ ;  $F_{1,10} = 22.70$ ,  $p = 0.0008$ ). In contrast, *P. glandulosa* trees were smaller ( $236 \pm 57.6 \text{ cm}^2$ ) and had a shrubby canopy with more stems at the base and branching starting at a lower height ( $0.67 \pm 0.05 \text{ m}$ ). Height and canopy related variables (leaf-area index, coefficient of light diffusion, and canopy diameter) were statistically similar between both nurse species.

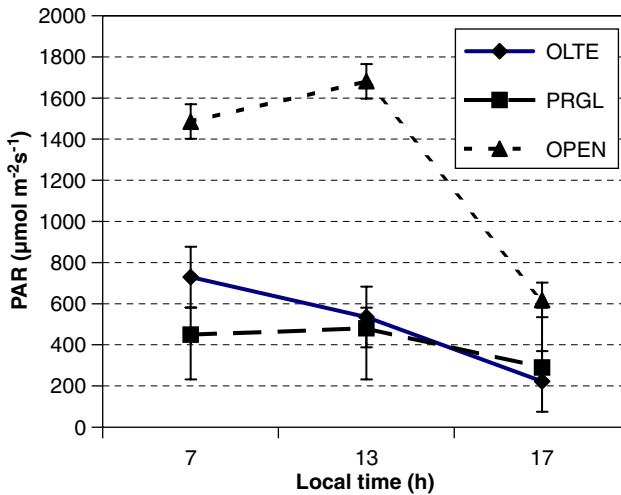


Fig. 2. Comparisons of photosynthetic active radiation (PAR) measurements (photosynthetic flux density in  $\mu\text{mol m}^{-2}\text{s}^{-1}$ ) in sites beneath *Oleña tesota* (OLTE), *Prosopis glandulosa* (PRGL) and in open spaces (OPEN) recorded the June 25, 1993.

### 3.4. Soil conditions

The MANOVA analysis of soils nutrients detected no significant differences under the nurse plant canopies of *O. tesota* and *P. glandulosa* (Wilks  $\lambda = 0.079$ ,  $F_{5,6} = 4.328$ ,  $p = 0.130$ ). Even independent analysis of organic matter, percent nitrogen, phosphorus, sodium and calcium under the canopies of both species were not significant. Litter accumulation was higher in the cages beneath *P. glandulosa* canopies as indicated by an ANOVA ( $F_{1,36} = 11.35$ ,  $p = 0.018$ ).

### 3.5. Abundance of bird nests on nurse plants

We found 35 nests on nurse trees belonging to three species of birds recorded as avian dispersers of *P. pringlei* seeds: 28 of these nests were built by *A. flaviceps* (Verdin), 5 by *Campylorhynchus brunneicapillus* (Cactus Wren), and 2 by *Zenaida asiatica* (White-Winged dove). The nurse tree on which more bird nests were found was *O. tesota* (17), compared to only one on *P. glandulosa*, which was built by a White-Winged dove. Nests of *C. brunneicapillus* were built in *P. pringlei* as well as in *Opuntia fulgida*, *Opuntia bigelovi* and *Stenocereus thurberi*. Only one nest of *Z. asiatica* was found on a *P. pringlei*. Disproportionately more nests were found on *O. tesota* than expected by relative cover of nurse plants at the study site ( $\chi^2 = 102.7$ , 3 df;  $p \ll 0.00001$ ; Table 1).

## 4. Discussion

The recruitment, growth and survival of *P. pringlei* seedlings transplanted under the two nurse species contrast with the natural spatial distribution of carbon that



Table 1

Abundance and canopy cover of cardon nurse species at Rancho San Germán, Sonora, Mexico, and number of nests of the verdin (*Auriparus flaviceps*), the main disperser of cardon, expected on the basis of relative canopy cover and observed, on nurse canopies in summer 1993

Nurse species	Abundance	Canopy cover (m <sup>2</sup> /0.2 ha)	Relative canopy cover	Expected nests	Observed nests
<i>Larrea tridentata</i>	67	120.88	0.42	12	0
<i>Jatropha cuneata</i> <sup>a</sup>	18	37.18	0.13	4	0
<i>Jatropha cinerea</i> <sup>a</sup>	11	20.53	0.07	2	0
<i>Prosopis glandulosa</i>	8	56.28	0.20	5	0
<i>Bursera microphylla</i> <sup>b</sup>	4	7.90	0.03	1	5
<i>Cercidium microphyllum</i> <sup>b</sup>	1	7.07	0.02	1	2
<i>Olneya tesota</i> <sup>b</sup>	3	9.90	0.03	1	17
<i>Ziziphus obtusifolia</i> <sup>b</sup>	0	0.00	0.00	<1	3
Others <sup>b</sup>	6	28.785	0.10	3	1
Total	118	288.531	1.00	28	28

<sup>a</sup>Lumped in one category: *Jathopha* spp for  $\chi^2$  analysis.

<sup>b</sup>Lumped in category “Others” for  $\chi^2$  analysis.

we have documented at the same site as well as in all the coastal lands of Sonora (Suzán et al., 1996). *P. pringlei* seedlings are spatially associated primary with *O. tesota* (Sosa, 1997; West et al., 2000), while *P. glandulosa* serves only as a secondary nurse plant (Tewksbury and Petrovich, 1994). If *O. tesota* is the primary species that is spatially associated with cardon, why do *P. pringlei* seedlings tend to perform better under *P. glandulosa* than under *O. tesota*?

A possible factor explaining differences in survivorship and growth in height could be differential temperatures beneath nurses resulting from different leaf phenologies. *O. tesota* is partially deciduous and leafless in the season prior to summer rains or in winters with catastrophic freezes, while *P. glandulosa* is completely deciduous in winter (Turner, 1963; Nilsen et al., 1984). However, our experimental results indicated non-significant differences for soils and stem temperatures beneath *O. tesota* and *P. glandulosa* canopies for both summer and winter measurements. Freezing effects should also be discounted, because our experimental site in Southern Sonora is not located in the region of frequent catastrophic freezes.

Growth of *P. pringlei* seedlings during the study period suggested possible differential allometric expressions beneath *O. tesota* or *P. glandulosa* canopies (Reiss, 1991). Height differences in *P. pringlei* could be the result of a tendency during the summer growth period for the seedlings to reach higher into the shady environment of *P. glandulosa* canopies. However, differences in height alone do not indicate a better growth performance of cactus seedlings (Malda et al., 1999), since our combined growth index analysis barely differed among nurse plants. In addition, in spite of slight differences in the crown architecture of *P. glandulosa* and *O. tesota*, the LAI and related measurements did not differ between the two species. Therefore, shade intensity alone cannot explain the different behavior of the seedlings.

Soil composition beneath the canopies of the two nurses in our sites was relatively similar, contrary to what has been reported from a pot experiment (Carrillo-García et al., 2000). In that study, *P. glandulosa* soil had higher N, P, and C contents than *O. tesota* soil; and *P. pringlei* seedlings survived better and grew larger in soils collected beneath *P. glandulosa* canopies than on soils collected beneath *O. tesota* canopies. Thus, soil composition does not explain the association pattern observed in adult *P. pringlei* either. Microbial activity of soil beneath nurse canopies has been demonstrated as a feasible variable affecting cactus growth and survival; both *P. glandulosa* and *O. tesota* presented comparable percentages of arbuscular mycorrhizae (AM) colonization, 57% and 46%, respectively (Carrillo-García et al., 1999). However, further studies are needed to elucidate whether soil beneath different canopy species influence colonization of *P. pringlei* seedling roots by AM. Both, *O. tesota* and *P. glandulosa* have been reported to nodulate and fix nitrogen (Felker and Clark, 1980, 1981), so differences in nitrogen fixation is also not a plausible explanation of differential seedling performance. Finally, competition for water between *P. pringlei* seedlings and nurse trees should also be discarded because both nurse species are phreatophytic partially deciduous trees (Nilsen et al., 1984).

Alternatively, we propose that the higher establishment and recruitment of *P. pringlei* under *O. tesota* canopies in the field area is the result of differential seed dispersal. Most nests of *Auriparus flaviceps*, the main *P. pringlei* disperser in the study area (Sosa, 1997), were found on *O. tesota* canopies. Only one nest, belonging to *Z. asiatica*, was found on a *P. glandulosa* canopy. Apparently, *A. flaviceps* prefer *O. tesota* twigs for building their globose-chambered nests. We believe that the smaller spines (<1 cm long) of *O. tesota* are more suited for manipulation by the small size *A. flaviceps* compared to the larger spines (up to 4 cm) of *P. glandulosa*. Although several species of bird dispersers use *P. glandulosa*, *O. tesota* and other shrubs and trees as perches, nesting and feeding-chicks behavior (Olin et al., 1989) increase the probability of seed dropping. *A. flaviceps* sometimes initiate the building of more than one nest before the female chooses one (Bent, 1964). We were able to collect several *P. pringlei* seeds from the edges of nests that may have been dropped when feeding chicks, or were defecated.

In conclusion, the higher recruitment of *P. pringlei* beneath *O. tesota* trees cannot be related to differential qualities of canopies or related soils in providing the seedlings with better micro-environmental or soil conditions. Instead, differential seed dispersal apparently accounts for the primacy of *O. tesota* as a nurse tree. Therefore, our study suggests that the relationships of cacti and nurse species are primarily the result of intricate biotic relationships rather than differences in simple physical conditions. These results provide the basis for extremely interesting further studies that need to consider the changing biotic relationships over longer periods of time.

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