

Spatial associations, size–distance relationships and population structure of two dominant life forms in a semiarid enclave of the Venezuelan Andes

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Abstract

The role of three thorny legume species as nurse plants and competitive relationships with columnar cacti were evaluated in a semiarid enclave of the Venezuelan Andes. Abundance and size of three columnar cacti species (*Stenocereus griseus*, *Cereus repandus* and *Pilosocereus tillianus*) under isolated shrubs of three thorny legumes species (*Prosopis juliflora*, *Acacia farnesiana* and *A. macracantha*) were recorded and compared with open areas. Using size–distance data we inferred the intensity of intra- and interspecific competition between both life forms in a “cardonal” (xeric zone) and “espinar” (mesic zone) of the enclave. Sixty-one columnar cacti were found beneath the three thorny legume species (92%), while only 5 cactus individuals were found in open areas (8%). Comparison of observed and expected number of cactus individuals shows that *S. griseus* and *C. repandus* are significantly associated with isolated shrubs of *A. farnesiana* and *A. macracantha*. Although *P. juliflora* contributed more than 40% of the total legume plant cover, the number of columnar cacti under its isolated shrubs was significantly lower than would be expected by chance. In all, 19 of 21 possible plant–plant combinations between and within columnar cacti and legume shrubs were recorded (espinar: 18, cardonal: 13, common combinations: 12). In both zones, intra- and interspecific combinations among columnar cacti species were relatively high (positive correlation between the sum of neighbour plant sizes and the distances separating them). Our results strongly suggest, at least for case of *S. griseus* and *C. repandus*, that these columnar cacti species require nurse plants for their establishment. The results on interference need still support from further research. We discuss the effects of plant–plant positive interactions on natural regeneration of these columnar cacti.

Introduction

Positive interactions between plants can determine community structure and local diversity in many habitats (Callaway 1995, 1997; Callaway and Walker 1997; Tewksbury and Lloyd 2001). One of such positive interactions is the so-called nurse syndrome, in which certain plants have a positive

influence on other plants (McAuliffe 1988; Bertness and Callaway 1994). The effect of a nurse plant depends on size/geometry of the benefactor plant (Franco and Nobel 1989; Valiente-Banuet and Ezcurra 1991; Tewksbury et al. 1999) and the size and position of the beneficiary plant under the nurse plant (Franco and Nobel 1989). Evergreens and plants with dense canopies such as thorny

mimosoid legumes have been found to be better benefactors compared to other growth forms, such as deciduous shrubs and plants with little ramifications (de Viana et al. 2001; Tewksbury and Lloyd 2001; Flores and Jurado 2003). Among all the positive plant–plant interactions, the association between cacti and their nurse plants becomes even more important since the beneficiary plant, the cactus, could in the medium or long term, compete or interfere with the benefactor plant, occupying its place in the ground (McAuliffe 1984; Yeaton and Romero 1986; Valiente-Banuet et al. 1991; Flores-Martínez et al. 1994). The canopy of nurse plants can foster the presence of a greater number of beneficiary plants compared to open spaces without shade and can influence the recruitment, growth, and spatial associations of columnar cacti (Valiente-Banuet and Ezcurra 1991; Mills et al. 1993; Tewksbury et al. 1999).

Arid environments are characterized by scarce water availability, the most important limiting factor for plant growth (Ehleringer 1984; Nobel 1988). Dominant plants of these habitats, such as thorny mimosoid legumes and/or columnar cacti, can compete for water in some stage of their growth (e.g. Yeaton and Cody 1976; Briones et al. 1996). Severe water conditions (xeric zones) could favor more facilitation than competition between neighbouring plants; thus, under benign water conditions (mesic zones), competition can be more intense than in abiotically stressful conditions (stress-gradient hypothesis, *sensu* Callaway 1997). However, recent meta-analysis suggests that some results will be unexpected and largely inconsistent with this hypothesis (Goldberg et al. 1999; Maestre et al. 2005). The effects of competition in arid plant communities can be inferred from the study of the relationship between distance and size of neighbouring plants (Pielou 1962; Fowler 1986; Welden et al. 1988; Wilson 1991; Briones et al. 1996). The hypothesis is that competition between neighbours results in density-dependent growth and mortality; thus, closely spaced plants will be small and have low survivorship (Pielou 1962; Fowler 1986). A positive correlation between the sum of neighbour plant sizes and the distances separating them can be interpreted as the result of competition, and the lack of such correlation as the result of the absence of competition (Pielou 1962; Yeaton and Cody 1976; Briones et al. 1996).

The Andes of northern South America contain a set of dry valleys with climatic characteristics that result from orographic rainfall shadows (Sarmiento 1975). These arid valleys constitute an archipelago of small arid enclaves that occur in the Andes from the Cordillera de Mérida (western Venezuela) to Ecuador through of Colombia mountain chains (Soriano and Ruíz 2002). The Lagunillas semiarid enclave, the bigger enclave of Venezuela (262 km²), contain thorny mimosoid legumes such as *Prosopis juliflora*, *Acacia farnesiana* and *A. macracantha* and columnar cacti, such as *Stenocereus griseus*, *Cereus repandus* and *Pilosocereus tillianus*. Both life forms are characteristic elements of this landscape that can reach heights of 7–9 m (Soriano and Ruiz 2002). Abundance of these plant species and water conditions of the enclave cause a gradient of mesic (locally known as “espinar”) and xeric (“cardonal”) zones. As in other arid semiarid zones, the legumes species can be important elements of the enclave because their canopy affords shade that could facilitate the establishment of columnar cacti seedlings (see Sosa and Fleming 2002 and Flores and Jurado 2003 for a detailed list of the reported associations), suggesting that the so-called nurse syndrome may be a plant–plant interaction frequent in these habitats. On the other hand, because low water availability and the hydric gradient that causes it, size–distance relationships between legumes and columnar cacti can be different in xeric and mesic zones. Thus, benefactor plants will be more important for columnar cacti recruitment in xeric than mesic zones and depending of benefactor plant size, columnar cacti can be potential competitors for thorny legumes that grow in both zones.

In this work, we examined the interactions between thorny mimosoid legumes and columnar cacti in a semiarid enclave of Venezuela. Specifically, we aim at answering the following three questions: (1) Is there greater spatial association between columnar cacti and legumes than expected by chance? (2) How are the size–distance relationships between thorny mimosoid legumes and columnar cacti in xeric and mesic sites? and (3) What is the population structure of main thorny legume and columnar cacti species of the enclave? We evaluated the hypotheses that beneath thorny legumes species the number of columnar cacti can be higher than in open areas, and size–distance relationships between legumes and

cacti could be more intense in mesic environments where positive effects of nurse syndrome can be neutral or very low.

Study area

This study was conducted in a mesic zone and in a xeric zone in the Lagunillas semiarid enclave in the Venezuelan Andes. The region shows a water deficit most of the year. Annual rainfall ranges from 450–550 mm with peaks in April–May and September–October, and a lengthy dry period from December to March. The enclave is characterized by a warm climate and contains different community types along a moisture gradient, from very arid to more mesic zones. The landscape is characterized by the presence of thorny mimosoid legumes (*P. juliflora* DC., *A. farnesiana* (Willd.) L., and *A. macracantha* H.B.K.) and columnar cacti species (*S. griseus* (Haw.) F. Busxb., *C. repandus* (L.) Backeb., and *P. tillianus* Gruber and Schaftzl), which can form two ecological subunits. The first type, locally known as “cardonal”, contains abundance of columnar cacti as well as high portions of open areas causing a xeric landscape strongly dominated by cacti. The second type, known as “espinar”, contains high abundances of thorny legume species whose umbrella-shape crowns form a dense thorny scrub associated, mainly, to the water bodies of the enclave. There is not difference in rainfall between both subunits. Our xeric zone (“cardonal”) was located near the Puente Real (8°28′30″ N and 71°24′26″ W), 4.5 km south-west of San Juan de Lagunillas, at an altitude of 720 m. Our mesic zone (“espinar”) was located near the Laguna de Caparú (8°29′16″ N and 71°20′10″ W), 3 km south-east of San Juan de Lagunillas, Mérida State, at an altitude of 780 m. As in other arid regions, natural vegetation has been replaced by cultivation and extensive grazing by cows and goats. Grazing and removal of taller thorny legumes have increased the processes of erosion and desertification in both zones.

Methods

Thorny legumes as nurse plants for columnar cacti

We selected both in a xeric as well as in a mesic zone, mature individuals of three thorny legume species that occur naturally there. We chose indi-

viduals with partially or completely isolated canopies to avoid the influence of adjacent neighbors. Shrubs with isolated crowns were scarce in both zones causing a relatively low sample size, although sufficient to assess the existence of nurse syndrome (*P. juliflora*: 20, *A. farnesiana*: 20, and *A. macracantha*: 12). In each case, the number of columnar cacti was recorded through one 1-m² quadrat randomly placed under the canopy of each thorny shrub. The space under the canopy of each shrub was divided in four quadrants and one was chosen randomly to lay out the 1-m² quadrat. In each quadrant, the presence and abundance of columnar cacti was recorded including size of each cactus.

Open areas without the influence of other trees/shrubs' crowns were sampled as control. These quadrats were randomly installed. A 100-m linear transect was placed in both xeric and mesic zones of our study site. Ten quadrats were evaluated in each zone. Quadrats were chosen through two random numbers that we placed considering the 100-m linear transect. The first number was placed on the linear transect (1–100 m), the second number was placed perpendicularly to the linear transect (1–25 m). For each second number, we alternated the direction of the perpendicular line between right and left. Maximum distance of the perpendicular line was 25 m. This distance was required to place 20 quadrats in open areas.

To determine if columnar cacti were randomly distributed among thorny mimosoid legume species, we assessed the cover of potential nurse plant by conducting circular plots of 9.0 m radius (~256 m², 41 circular plots in total), following the logarithmic plot method (McAuliffe 1990). If columnar cacti were distributed randomly with respect to thorny legume species, the expected distribution of columnar cacti among nurse plants should be proportional to cover provided by each potential nurse-plant species. Chi-square test (χ^2) was carried out to test the null hypothesis that the number of columnar cacti under each species is proportional to the total area covered by the canopy of each thorny legume species. The standardized residuals were used to test the significance of each cell where any value greater than 2 was regarded as a significant deviation of residuals normal distribution. Differences in size of columnar cacti for each thorny legume species were analyzed through Kruskal–Wallis and Mann–Whitney tests.

Size–distance relationships between thorny legumes and cacti

An indirect approach to assess intra- and inter-specific competition between both life forms was used. Although plant size can also be related to the demographic/morphological stage of the plant, we assumed that closely spaced plants will be small as a consequence of density-dependent growth and mortality; consequently, closely spaced plants will be small and have low survivorship (Pielou 1962; Fowler 1986).

Nine 200-m² plots (1800 m²) and eight 200-m² plots (1600 m²) were installed in the xeric and mesic zones, respectively. All plants of the three thorny legume species and three columnar cacti species in each plot were taken as focal plants. Species identity, sizes and distance between each focal plant and its nearest neighbour were recorded for each pair of plants. For thorny legumes species, we used the canopy radius as size measurement because of a positive correlation between height and canopy radius ($n = 52$, $r = 0.72$, $p < 0.0001$). For columnar cacti species, we used main stem height as size measurement. When two plants were each other's nearest neighbour the same set of readings was used twice. When the nearest neighbour of a focal plant was outside the limits of the plot, its size and the distance between them were recorded and included in the analysis (e.g. Briones et al. 1996). Cactus individuals growing around or from fallen stems of cacti were recorded as vegetative propagation. If several asexual recruitments were found growing clumped among them, the vegetative cactus with higher size was chosen.

All data were sorted into pairs of intra- and interspecific species combinations. Twenty-one pairs of combinations of interactions between thorny legumes and columnar cacti species were expected. This means that nearest-neighbour pairs were identified as belonging to only one of these categories. The sizes of both plants in each pair were added up, and the regressions of these sums of neighbour plant-sizes on the distances separating them were calculated for every intra- and interspecific species combination. The normality of both variables, sum of sizes and distance, was obtained through a \log_{10} transformation. Since plant density and size may affect the slope of the relationship between sum of sizes and distances (Wilson 1991), data (\log_{10} sum of sizes and \log_{10}

distances) were standardized by dividing each value by the average calculated within each species combination; thus, each standardized variable had a mean of 1 (Wilson 1991; Briones et al. 1996).

In order to test if the intensity of competition is symmetric within each interspecific combination, two separate regressions (one for each species of pair) between plant size and distance were performed after the transformation and standardization of both variables were conducted. If the two regression slopes were different from zero, significant differences between the slopes would indicate asymmetry in the competition intensity experienced by both species. If only one slope was different from zero asymmetry could be inferred because the size of one species varies with distance, whereas the other did not. Finally, if the two regression slopes were not different from zero, asymmetry could not be inferred (*sensu* Briones et al. 1996). Differences between coefficients of correlation (r) were taken as differences of the importance of competition (Wilson 1991; Briones et al. 1996).

Size structure

The nine 200-m² plots (1800 m²) and eight 200-m² plots (1600 m²) installed in the xeric and mesic zones were used to assess the relative abundance and frequency distribution of the main species that occur in both sites, i.e., *S. griseus* and *C. repandus* as the more abundant columnar cacti for each site, and *P. juliflora* as the more conspicuous thorny legume shrub in both zones. Differences in relative abundance between mesic and xeric zones were evaluated through *t*-tests for independent samples by groups. Chi-square (χ^2) test was carried out to test the null hypothesis that the frequency distribution of each species is proportional to the exponential distribution expected by random. Statistica package (version 6.0) was used in all cases.

Results

Thorny legumes as nurse plants for columnar cacti

In all, 61 columnar cacti were found beneath the three thorny legume species (92%), while only 5 cactus individuals were found in open areas (8%) ($\chi^2 = 98.69$, d.f. = 6, $p < 0.0001$). For the 61

columnar cacti located under legume shrubs, 32 cacti (52.5%) were found under the canopies of *P. juliflora*, 23 cacti (37.7%) beneath *A. farnesiana* and 6 cacti (9.8%) under *A. macracantha*.

Comparison of observed and expected number of cactus individuals growing beneath legume shrubs shows that *S. griseus* and *C. repandus* were significantly associated with *A. farnesiana* and *A. macracantha*. Although *P. juliflora* contributed more than 40% of the total legume plant cover, the number of columnar cacti under its isolated shrubs was significantly lower than would be expected from its cover. For each cactus species, the open area had a significantly lower number of individuals than expected by chance (Figure 1).

Isolated shrubs of *A. farnesiana* and *A. macracantha* were scarce in the mesic zone. For this reason, we only analyzed differences in number of columnar cacti beneath isolated shrubs of *P. juliflora* growing in the xeric and mesic zones. Shrubs of *P. juliflora* contributed from 34.5% (xeric) to 48.8% (mesic) to total legume plant cover; however, the number of cactus individuals beneath its isolated shrubs was not significantly greater than expected by chance (absolute values < 2).

The size of columnar cacti species growing under canopies of the three thorny legume species was different ($H_{(2,61)}=7.5$, $p=0.02$). The size of columnar cacti was significantly greater under the canopy of *A. farnesiana* ($1.16 \text{ m} \pm 1.02$, mean \pm SD) and *A. macracantha* ($1.57 \text{ m} \pm 1.43$) than under *P. juliflora* crown ($0.59 \text{ m} \pm 0.78$) (Tukey type test: $p < 0.05$).

No difference was found between columnar cacti height growing under the canopy of *A. farnesiana* ($U=34$, $p=0.06$) and *A. macracantha* ($U=2$, $p=0.35$). In contrast, size of columnar cacti species growing under canopy of *P. juliflora* was significantly different ($H_{(2,32)}=6.13$, $p=0.04$). Size of *S. griseus* cacti ($0.84 \text{ m} \pm 0.87$) was significantly bigger than *C. repandus* ($0.59 \text{ m} \pm 0.86$) and *P. tillianus* cacti ($0.14 \text{ m} \pm 0.06$) (Tukey type test: $p < 0.05$).

No difference was found between the height of columnar cacti that grow under the canopy of *P. juliflora* in the mesic zone ($H_{(2,18)}=0.45$, $p=0.79$) and cacti growing under *P. juliflora* in the xeric zone ($U=10.5$, $p=0.11$); however, the size of columnar cacti species growing under canopies of *P. juliflora* in the xeric zone ($0.96 \text{ m} \pm 0.99$) was significantly greater than the size of cacti species

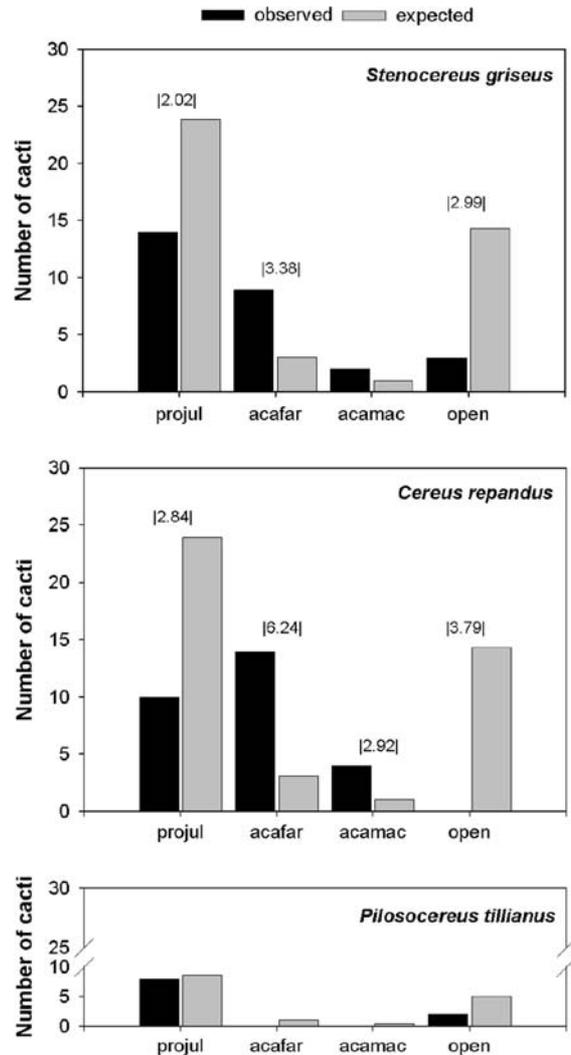


Figure 1. Observed and expected columnar cacti growing beneath the canopy of three thorny legume species and open areas without shade in a semiarid enclave of the Venezuelan Andes. Absolute values showed are significant at 5% of the normal distribution (standardized residuals test). Projul = *Prosopis juliflora*, acafar = *Acacia farnesiana*, acamac = *Acacia macracantha*, open = Open space.

that grow under *P. juliflora* in mesic zone ($0.31 \text{ m} \pm 0.42$) ($U=56$, $p=0.01$).

Size–distance relationships between thorny legumes and cacti

In both zones, 19 of 21 combinations were recorded (Tables 1 and 2). Nevertheless, we only recorded one or two pairs of some combinations;

Table 1. Mean $\log_{10} S_c$ (sum of plant size) and $\log_{10} D$ (nearest neighbour distance) values between three thorny mimosoid legumes species (*Prosopis juliflora*, *Acacia farnesiana* and *A. macracantha*) and three columnar cacti species (*Stenocereus griseus*, *Cereus repandus* and *Pilosocereus tillianus*) in a mesic arid zone of the Venezuelan Andes.

Species combination	No. of pairs	$\log_{10} S_c$ (cm)	$\log_{10} D$ (cm)
<i>P. juliflora</i> – <i>S. griseus</i>	78	2.3809	1.8564
<i>P. juliflora</i> – <i>C. repandus</i>	4	2.8460	2.1398
<i>P. juliflora</i> – <i>P. tillianus</i>	54	2.5729	1.8190
<i>A. farnesiana</i> – <i>S. griseus</i>	7	2.3556	1.7307
<i>A. farnesiana</i> – <i>C. repandus</i>	2	2.8853	2.0212
<i>A. farnesiana</i> – <i>P. tillianus</i>	4	2.3804	1.8528
<i>A. macracantha</i> – <i>S. griseus</i>	7	2.2127	1.8482
<i>A. macracantha</i> – <i>C. repandus</i>	1	2.6434	2.0569
<i>A. macracantha</i> – <i>P. tillianus</i>	12	2.2728	1.8477
<i>P. juliflora</i> – <i>A. farnesiana</i>	2	2.6051	1.8972
<i>P. juliflora</i> – <i>A. macracantha</i>	0	–	–
<i>A. farnesiana</i> – <i>A. macracantha</i>	0	–	–
<i>P. juliflora</i> – <i>P. juliflora</i>	15	2.5641	1.7933
<i>A. farnesiana</i> – <i>A. farnesiana</i>	0	–	–
<i>A. macracantha</i> – <i>A. macracantha</i>	3	2.2148	1.4072
<i>S. griseus</i> – <i>C. repandus</i>	32	2.2584	1.6433
<i>S. griseus</i> – <i>P. tillianus</i>	194	2.1950	1.6342
<i>C. repandus</i> – <i>P. tillianus</i>	3	1.7229	1.8124
<i>S. griseus</i> – <i>S. griseus</i>	629	2.1501	1.5533
<i>C. repandus</i> – <i>C. repandus</i>	1	2.4456	2.2406
<i>P. tillianus</i> – <i>P. tillianus</i>	150	2.2276	1.4679
Total	1198		

Table 2. Mean $\log_{10} S_c$ (sum of plant size) and $\log_{10} D$ (nearest neighbour distance) values between three thorny mimosoid legumes species (*Prosopis juliflora*, *Acacia farnesiana* and *A. macracantha*) and three columnar cacti species (*Stenocereus griseus*, *Cereus repandus* and *Pilosocereus tillianus*) in a xeric arid zone of the Venezuelan Andes.

Species combination	No. of pairs	$\log_{10} S_c$ (cm)	$\log_{10} D$ (cm)
<i>P. juliflora</i> – <i>S. griseus</i>	20	2.3186	1.9072
<i>P. juliflora</i> – <i>C. repandus</i>	30	2.5522	1.9871
<i>P. juliflora</i> – <i>P. tillianus</i>	0	–	–
<i>A. farnesiana</i> – <i>S. griseus</i>	8	2.5427	1.8860
<i>A. farnesiana</i> – <i>C. repandus</i>	6	2.4944	1.6746
<i>A. farnesiana</i> – <i>P. tillianus</i>	1	2.6042	2.1461
<i>A. macracantha</i> – <i>S. griseus</i>	1	2.6532	2.1461
<i>A. macracantha</i> – <i>C. repandus</i>	2	2.2549	2.2982
<i>A. macracantha</i> – <i>P. tillianus</i>	0	–	–
<i>P. juliflora</i> – <i>A. farnesiana</i>	0	–	–
<i>P. juliflora</i> – <i>A. macracantha</i>	1	5.0099	2.3222
<i>A. farnesiana</i> – <i>A. macracantha</i>	0	–	–
<i>P. juliflora</i> – <i>P. juliflora</i>	20	2.5211	2.0980
<i>A. farnesiana</i> – <i>A. farnesiana</i>	0	–	–
<i>A. macracantha</i> – <i>A. macracantha</i>	0	–	–
<i>S. griseus</i> – <i>C. repandus</i>	44	2.3740	1.8918
<i>S. griseus</i> – <i>P. tillianus</i>	0	–	–
<i>C. repandus</i> – <i>P. tillianus</i>	1	2.7582	2.3222
<i>S. griseus</i> – <i>S. griseus</i>	19	2.3879	1.8442
<i>C. repandus</i> – <i>C. repandus</i>	92	2.3617	1.7836
<i>P. tillianus</i> – <i>P. tillianus</i>	0	–	–
Total	245		

for this reason, we divided pairs recorded in three types of combinations: (1) Combinations that existed in each zone in very low frequency, i.e., amount insufficient for size–distance analysis, (2) Combinations that existed in each zone in low or intermediate frequency, insufficient to detect tendencies statistically different in size–distance analysis, and (3) Combinations that existed in each

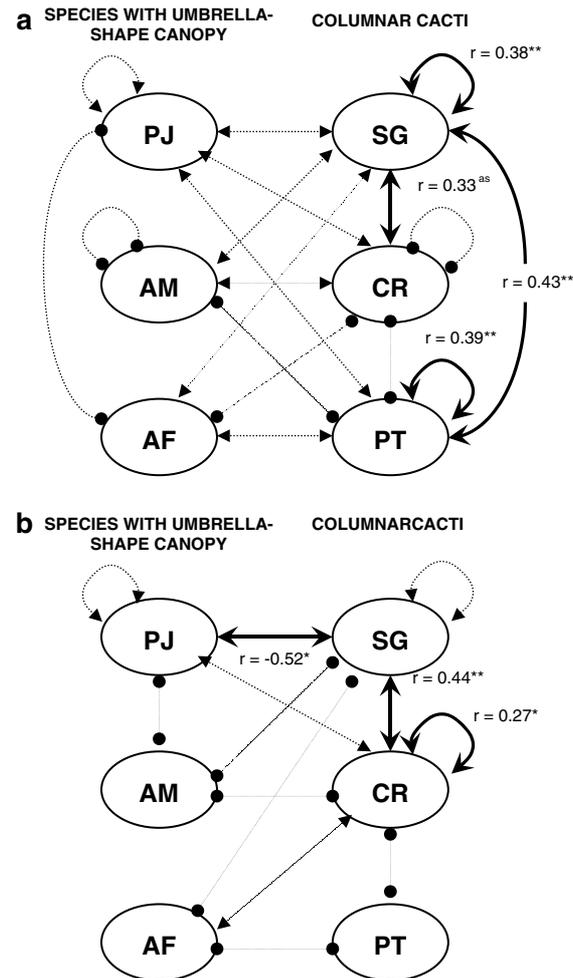


Figure 2. Relations between three thorny legume species and three columnar cacti on mesic (a) and xeric (b) sites in an arid zone of the Venezuelan Andes. Lines represent existence of pairs for each combinations: (●–●) represent relations that existed but with lower frequency; (◄–►) represent relations that existed but without tendencies statistically different and ((◄–►)) represent higher relations in each site with positive correlations suggesting intra- or interspecific competition. PJ: *Prosopis flexuosa*, AF: *Acacia farnesiana*, AM: *Acacia macracantha*, SG: *Stenocereus griseus*, CR: *Cereus repandus*, PT: *Pilosocereus tillianus*. Significance for each positive combination is * $p < 0.05$, ** $p < 0.01$ and as = almost significant, $p = 0.06–0.07$.

zone in high frequencies, enough to show correlations statistically significant (Figure 2a, b).

In mesic zone, 18 of 21 possible combinations were recorded (Table 1). Only four combinations showed a significant positive correlation in the relationship between the standardized \log_{10} sum of sizes and standardized \log_{10} distance (Figure 2a). The variation in size accounted for by distance was higher for intra- and interspecific combinations in three columnar cacti, i.e., the coefficient of determination in columnar cacti pairs were greater than in their combinations with thorny legumes or intraspecific legume combinations. The slope of the size–distance regression was 0.3471 ($r^2 = 0.11$, $p = 0.06$) (*S. griseus*–*C. repandus*) and 0.3515 ($r^2 = 0.18$, $p < 0.0001$) (*S. griseus*–*P. tillianus*) for interspecific combinations, and 0.3003 ($r^2 = 0.15$, $p < 0.0001$) (*P. tillianus*–*P. tillianus*) and 0.3392 ($r^2 = 0.14$, $p < 0.0001$) (*S. griseus*–*S. griseus*) for interspecific combinations. In both cases, our results show *S. griseus* as a relatively important species in size–distance relationships between columnar cacti. When the symmetry was analyzed no combination, except *S. griseus*–*C. repandus*, showed asymmetry, i.e., the size of *S. griseus* increased significantly with distance whereas the size of *C. repandus* did not (Table 3). For all other combinations, the sizes of species interacting were not affected by distance.

In the xeric zone, 13 of 21 combinations were recorded (Table 2). Among them, only two combinations showed a significant positive correlation in the relationships between the standardized \log_{10} sum of sizes and standardized \log_{10} distance (Figure 2b). Besides, the *P. juliflora* and *S. griseus* combination showed a significant negative correlation that suggests that small cacti are associated to *P. juliflora* shrubs with intermediate or higher canopies ($r = -0.52$, $p < 0.05$). As in the mesic zone, the variation in size accounted for by distance was higher for intra- and interspecific combinations in two of three columnar cacti. The slope of the size–distance regression was 0.1873 ($r^2 = 0.07$, $p = 0.01$) (*C. repandus*–*C. repandus*) and 0.2957 ($r^2 = 0.19$, $p = 0.003$) (*S. griseus*–*C. repandus*); however, when the effect of distance between neighbours over the plant size of each species was analyzed within each combination, only for *S. griseus*–*C. repandus* couples we inferred asymmetry in its size–distance relationships; specifically, as in the mesic zone the size of *S. griseus* increased significantly with dis-

Table 3. Slope of regressions between plant size and distance to the nearest neighbour. Results for thorny legume–columnar cacti combinations are shown for an arid zone of the Venezuelan Andes.

Species combination	Species in focus	<i>n</i>	Slope
MESIC SITE			
<i>Stenocereus griseus</i> – <i>Pilosocereus tillianus</i>	<i>Pilosocereus</i>	194	0.3766**
	<i>Cereus</i>	194	0.5189**
<i>Cereus repandus</i> – <i>S. griseus</i>	<i>Cereus</i>	32	0.1794 ns
	<i>Stenocereus</i>	32	0.5412*
<i>S. griseus</i> – <i>S. griseus</i>	<i>Stenocereus</i>	629	0.3764**
	<i>Stenocereus</i>	629	0.4282**
<i>P. tillianus</i> – <i>P. tillianus</i>	<i>Pilosocereus</i>	150	0.2796**
	<i>Pilosocereus</i>	150	0.4372**
XERIC SITE			
<i>Prosopis juliflora</i> – <i>S. griseus</i>	<i>Prosopis</i>	20	–0.0575 ns
	<i>Stenocereus</i>	20	–0.1068 ns
<i>C. repandus</i> – <i>S. griseus</i>	<i>Cereus</i>	44	0.2403 ns
	<i>Stenocereus</i>	44	0.3778*
<i>C. repandus</i> – <i>C. repandus</i>	<i>Cereus</i>	92	0.2174*
	<i>Cereus</i>	92	0.2645**

* $p < 0.05$, ** $p < 0.01$ and ns = $p > 0.05$.

tance whereas the size of *C. repandus* did not. The slopes of the size–distance regression in *S. griseus*–*C. repandus* combination between both zones was not significantly different (Difference test, $p > 0.05$).

In both zones the more frequent combinations were intraspecific cacti couples (Tables 1 and 2). In the mesic zone, the more frequent combination was *S. griseus*–*S. griseus* with 629 pairs (52%). In contrast, in the xeric zone the most frequent combination was *C. repandus*–*C. repandus* with 92 pairs (38%). In no case was competition demonstrated suggesting intraspecific association in each zone without conclusive evidence of competition or interference between individuals participating in each interaction.

Size structure

The three thorny legume species showed different abundances in each zone. In all, 85 individuals of *P. juliflora*, 13 of *A. macracantha* and 7 of *A. farnesiana* were recorded in the mesic zone. In contrast, 42 individuals of *P. juliflora*, 1 of *A. macracantha* and 6 of *A. farnesiana* were recorded in the xeric zone. The relative abundance of *P. juliflora* shrubs was significantly higher in the mesic (10.6 shrubs/200-m² plot \pm 3.07, mean \pm DS) compared to the xeric zone (4.7 shrubs/200-m² plot \pm 3.39) ($t = -3.78$, $p = 0.002$).

The relative abundance of *S. griseus* was significantly greater in the mesic zone (99.1 cacti/200-m² plot \pm 33.5, mean \pm DS) than the abundance of *C. repandus* in the xeric zone (14.8 shrubs/200-m² plot \pm 6.23) ($t = -7.42$, $p < 0.0001$). Even though data distribution tend to be positive exponential for *S. griseus* and *C. repandus* in the mesic and xeric zones (Figure 3), the frequency distribution in both species in the two zones was significantly different from the exponential distribution expected by random (Chi square test, $p < 0.05$ for all cases). These frequency distributions suggest stable populations at least for the distribution of their individuals by size range. In all, four populations showed high proportion of young cacti < 1.0 m of height and low amount of old cacti, i.e. cacti between 5 and 6 m in height (Figure 3). At least one-fifth of both *S. griseus* and *C. repandus* populations showed individuals < 0.5 m in height. Proportion of *S. griseus* individuals < 0.5 m in height was significantly higher in the mesic (28.7%) than in the xeric zone (19.8%) (Proportion test, $p = 0.04$). In contrast, the proportion of *C. repandus* individuals < 0.5 m height was not significantly different between the mesic (22.5%) and xeric zones (17.9%) (Proportion test, $p > 0.05$). These results suggest higher natural regeneration of *S. griseus* seedlings in the mesic than in the xeric zone, and habitat independence for establishment of *C. repandus* seedlings.

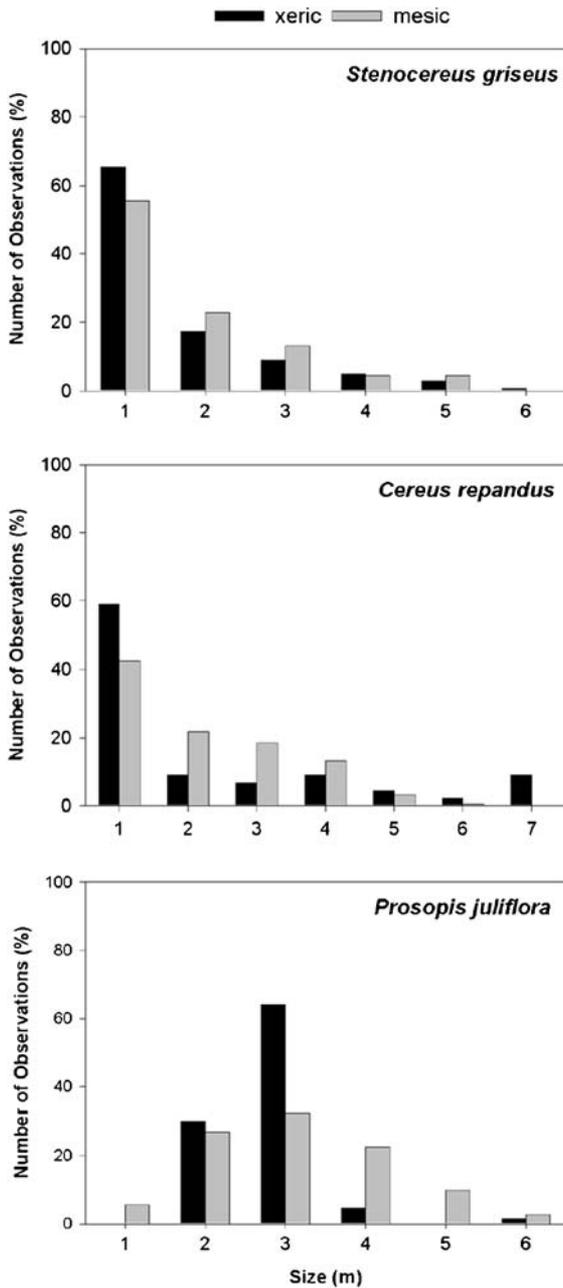


Figure 3. Population structure of *Prosopis juliflora*, *Stenocereus griseus* and *Cereus repandus* populations growing in a xeric and in a mesic zone in a semiarid enclave in the Venezuelan Andes.

Frequency distribution of *P. juliflora* showed that presence of individuals of intermediate and small sizes was low. As in populations of columnar cacti, frequency distribution in the two zones was significantly different from an exponential

distribution expected at random (Chi square test, $p < 0.05$). In the mesic zone, the frequency distribution had a unimodal curve with absence of individuals < 2 m of radius. In the xeric zone, the size structure of *P. juliflora* was still more anomalous than in the mesic zone. Individuals between 2 and 3 m of radius were common, while newly individuals < 2 m of size were not found in the field. These results suggest that seedling recruitment of *P. juliflora* in both zones is low.

Discussion

According to the results presented, there is suggestive evidence of the occurrence of the nurse plant phenomenon in the Venezuelan Andes. As we supposed in our hypothesis, results show that natural regeneration of columnar cacti beneath isolated shrubs of thorny legume species is higher in relation to open areas. This suggests that common underlying mechanisms may be operating, including seed dispersal by animals under canopies, post-germination mortality of seedlings in open areas restricting them to areas under shrubs canopies; and amelioration of physical conditions and modification of soil nutrient levels beneath plant canopies (McAuliffe 1988; Valiente-Banuet et al. 1991; Rossi and Villagra 2003). Although columnar cacti apparently could depend on nurse plants for natural regeneration, their distribution beneath potential nurse plants is highly non-random. Cactus individuals of *S. griseus* and *C. repandus* are found significantly nearer to isolated shrubs of *A. farnesiana* than would be expected by chance, suggesting the importance of this legume species for the establishment of these columnar cacti. In contrast, individuals of *P. tillianus*, a long-lived columnar cactus endemic of the enclave, are rarely recorded under the canopies of thorny legume species suggesting the relative contribution of so-called nurse syndrome to sexual reproduction of this cactus species.

Several studies have analyzed the establishment of succulents under potential nurse plants (Valiente-Banuet and Ezcurra 1991; Valiente-Banuet et al. 1991; Flores-Martínez et al. 1994; Rossi and Villagra 2003). Few of them have reported a lower number of beneficiaries than expected by chance (Valiente-Banuet et al. 1991). The high number of columnar cacti under *P. juliflora* is a consequence

of its greater cover in relation to *A. farnesiana* and *A. macracantha*. Although *P. juliflora* contributed more than 40% of the total legume plant cover, the number of columnar cacti under its isolated shrubs was significantly lower than would be expected by its cover. This suggests that other mechanisms may be regulating the relationships between cacti and these shrubs. In fact, ground-foraging ants of the genus *Pheidole* are strong seed consumers of *S. griseus* (Ibañez and Soriano 2005) and *C. repandus* (D. Larrea, unpublished data); however, the effects of these granivorous ants beneath *P. juliflora* shrubs are still unknown.

Plant cover provided by thorny legume species suggests greater availability of microsites for dispersed seed (Montiel and Montaña 2000; Howe and Miriti 2004). As in other arid regions, these perennial shrubs can be used as temporal shelters or perches by birds, bats and other small vertebrates. Thus, thorny legume shrubs could contribute to the distribution patterns providing safe places for seed dispersal of columnar cacti such as perch sites and shade for its main dispersers. In fact, *Glossophaga longirostris*, a nectarivorous, pollivorous, and frugivorous bat, and another glossophagine species, *Leptonycteris curasoae*, are important consumers of *S. griseus* and *C. repandus* fruits (Sosa and Soriano 1996; Soriano and Ruiz 2002). These bat species probably deposit seeds consumed of fruits under the crown of *P. juliflora* and *A. farnesiana* causing higher abundance of seeds under these woody plants than in open areas. Together with these bats, bird species such as *Melanerpes rubricapillus* and *Mimus gilvus* (Soriano et al. 1999) may allow non-random deposit of columnar cacti seeds. Therefore, similar to other arid regions of world (see Flores and Jurado 2003 for a detailed list of the reported associations), natural regeneration of columnar cacti under thorny legume species is an example that plant–plant positive associations also occurs in tropical semiarid zones; nevertheless, their variants, and the reasons that account for them still remain to be elucidated.

Even though *P. tillianus* tends to asexual reproduction, no evidence of vegetative propagation was found in cactus growing under isolated shrubs. Asexual reproduction in many arid-land succulent species can be a consequence of a very low production of viable seeds or can be related to environmental bottlenecks that drastically reduce

the establishment of seedling (Franco and Nobel 1989; Mandujano et al. 1996). Both aspects have been scarcely evaluated in the semiarid environments of the Venezuelan Andes (Sosa and Soriano 1996; Soriano and Ruiz 2002). More research is needed to determine under what conditions these columnar cacti may reproduce by vegetative propagation and how nurse plants help to survival and/or growth of sexually derived seedlings.

The relationships between sizes and distances of nearest-neighbour plants suggest that intraspecific interactions among columnar cacti can be more important than interspecific combinations. Size–distance pattern found in this study could be explained by adaptations of columnar cacti to use unevenly distributed soil water. Other studies in North American deserts also show that intraspecific could be more important than interspecific interactions. Yeaton and Cody (1976) investigated size–distance relationships between three species in the Mojave desert and found that intraspecific correlations were higher than interspecific correlations. Briones et al. (1996) used correlation coefficients between distances and sizes of neighbour plants to measure intra and interspecific competition between *Hilaria mutica*, *Larrea tridentata* and *Opuntia rastrera* in the Chihuahuan desert. They reported higher intra than interspecific correlations with r^2 -values from 0.07 to 0.61.

In contrast with the data mentioned above, our r^2 -values (0.07–0.19) show that the importance of intraspecific competition can be low. These r^2 -values also suggest that size–distance relationships between the species studied can be strongly non-linear. Although the normality of the sum of sizes and distance was obtained through a \log_{10} transformation, by taking the logarithm of both variables, some non-linear or exponential relationship tends to become linear; so complex non-linear relationships among potential competitors can be simplified. Thus, direct experiments should be conducted under natural conditions in the field for a better knowledge of negative interactions in this tropical semiarid enclave. In this sense, recently Armas et al. (2004) have proposed a new comparative linear index (relative interaction intensity, RII), which is based in measures of biomass and which is appropriate for use in parametric meta-analysis.

On the other hand, in the mesic zone the frequency of size–distance combinations between

thorny legume and columnar cacti species was low, except for *P. juliflora*–*S. griseus* (6.5%) and *P. juliflora*–*P. tillianus* couples (4.5%). In the xeric zone, combinations between both life forms were relatively high for *P. juliflora*–*C. repandus* (12.2%) and *P. juliflora*–*S. griseus* couples (8.2%), suggesting that cactus individuals will be favourably growing near trunks of *P. juliflora* shrubs, mainly under severe water conditions. Habitat under nurse plants canopies may act as an “environmental buffer”, providing homogeneous abiotic conditions to columnar cacti and other perennials and/or ephemeral species (Suzan et al. 1996; Tewksbury and Lloyd 2001). Thus, the existence of nurse plants for cacti sexual recruitment suggests that our semiarid landscape can be an environmental bottleneck, where dispersal efficiency and/or microclimatic conditions in some safe site can be a common process.

A high fruit production and a very low rate of sexual recruitment suggests asymmetry in the interaction between fleshy-fruits plants and frugivorous animals, where rewards for seed consumers are higher than advantages obtained by columnar cacti species (Schupp 1995; Montiel and Montaña 2000). Our analysis of frequency distribution by size category suggests that such asymmetry can be low or absent in both zones studied. Both populations of cacti, *S. griseus* in the mesic zone and *C. repandus* in the xeric zone, showed stable distributions with a high proportion of young cacti for replacement of old individuals. This type of population structure suggests growing populations that are regenerating constantly, in which mortality rate declines with size (Godínez-Álvarez et al. 2003). In contrast, both populations of *P. juliflora* show lack of small individuals suggesting very low rates of natural regeneration. Practically both populations are composed of small and median shrubs (2–4 m of canopy radius). Absence of seedlings and saplings can be a consequence of low rate of seed germination, or seed predation by bruchids. High seed predation has been reported in others species of the genus *Prosopis*. Seeds of *Prosopis flexuosa*, a nurse plant in the central Monte desert, Argentina, are severely consumed by *Dolichotis pataganum* (Caviidae) (Campos and Ojeda 1997) and, hence, this species does not tend to form a persistent seed bank (Villagra et al. 2002). Low presence of conspecific individuals under the *P. juliflora* canopy

suggests that recruitment occurs in pulses, which are likely associated with infrequent favourable conditions for seed germination and seedling establishment. Even though natural regeneration of *P. juliflora* tends to be low, other reasons may explain the anomalous structure of their populations, such as replacement of natural vegetation by cultivation, strong presence of cows and goats and, mainly, cutting of intermediate and higher thorny legumes.

In summary, our results strongly suggest the occurrence of the nurse plant phenomenon in semiarid enclaves of the Venezuelan Andes. Shrubs of *P. juliflora* and mainly of *A. farnesiana* could modify the spatial pattern of *S. griseus* and *C. repandus*. We can conclude that some cactus–nurse plant associations are highly non-random and should be considered essential for the development of a dynamic patch structure in the xeric zones. In contrast, our results on size–distance relationships are still far from conclusive because of the indirect approach used to measure competition. More research is needed to evaluate the mechanisms proposed to explain these positive and negative interactions. Progress in our understanding of these plant–plant relationships is crucial to enable prediction of the impacts of human perturbations on these Andean semiarid landscapes.

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