Positive interactions between columnar cacti and thorny legume species in a semi-arid enclave of the Venezuelan Andes (Final Report, Grant 17.01.06)

by Daniel M. Larrea-Alcázar

1. Introduction

Cacti are a very diverse plant family comprising more than 2000 species, most of which are native and endemic to arid and semi-arid environments of the Neotropical region. Most species of cacti grow spatially associated with mimosoid shrubs, which can modify soil properties and microclimate conditions below their crowns compared to surrounding open areas, and favour cactus germination and establishment. Although cacti-shrub associations have been well documented, our knowledge about the importance of the so-called nurse-plant syndrome phenomenon for the spatial arrangement and recruitment of long-lived columnar cacti species occurring in the Venezuelan Andes is still scarce.

Along the Andes of northern South America, several dry valleys occur which are geographically isolated, have similar physiognomy and constitute an archipelago of small semi-arid patches from Cordillera de Mérida (western Venezuela) through Colombia to Ecuador. The Lagunillas enclave, the biggest of this type in the Venezuelan Andes, contains mimosoid shrubs and columnar cactus species as the prevailing elements of its xerophyllous vegetation, which can form a habitat mosaic from xeric (cactus thicket) to mesic (thornscrub) sites. According to the stress-gradient hypothesis proposed by Bertness & Calllaway (1994), if facilitation prevails over competition, spatial association between cacti and perennial shrubs should be stronger in xeric than in mesic sites. There is suggestive evidence on the effect of these mimosoid shrubs on the spatial distribution of columnar cacti (Larrea-Alcázar & Soriano, 2006). However, there is no information on the dynamic of these plant-plant associations (mesic vs. xeric sites) and if other interactions are occurring at the enclave involving different growth forms of cacti.

In this work, differences in the cacti-shrub spatial association pattern and in two main post-dispersal processes (seed germination and early seedling survivorship) of two columnar cacti were studied in two contrasting habitats of an Andean semi-arid enclave. This information should help us to determine the overall importance of mimosoid species as nurse plants for the natural regeneration of cacti in this Andean semi-desert.

2. Study Area

This study was carried out in the Lagunillas semiarid enclave in the Venezuelan Andes (262 km2). Annual rainfall ranges from 450-550 mm, with peaks in April-May and September-October. Weather is semiarid and it is characterized by a warm climate with 22°C of annual mean temperature. The dominant vegetative elements of this semiarid landscape are mimosoid shrubs, such as *Prosopis juliflora* DC., *Acacia farnesiana* (Willd.) L. and *A. macracantha* H.B.K.; and columnar cactus species, such as *Stenocereus griseus* (Haw.) F. Busxb., *Cereus repandus* (L.) Backeb. and *Pilosocereus tillianus* Gruber & Schaftzl. In the lower stratum, together with small perennial and ephemeral plant species, the vegetation is characterized by the presence of globose cacti of genus *Mammillaria* and *Melocactus*. Among these, *Mammillaria mammillaris* (L) Karsten and *Melocactus schatzlii* Till & Gruber are the most abundant. Thornscrubs are strongly associated with small persistent water bodies of the enclave and contain high abundances of *P. juliflora* (~ 307 ind/ha), as well as scarce portions of bare areas (< 20%); while cactus thickets occur mainly on dry uplands and contain high abundance of *A. farnesiana* (~ 116 ind/ha), together with large portions of bare areas (30 -

35%). In the thornscrubs, soils are loamy clay with values of available water in the soil from 7.5% to 8.5%, while in the cactus thickets, soils are loamy sand with values of available water from 1.0% to 5.5%. Both habitats can represent 62% (cactus thicket) and 28% (thornscrub) of the total cover of the enclave and there is no difference in annual rainfall between them.

The study was conducted in five study sites within the enclave. Two study sites were located close to Caparú Lagoon (mesic sites – low water stress). We defined these zones as continuum thornscrub (Mesic 1) and low thornscrub (Mesic 2). Long-lived mimosoid shrubs in the continuum thornscrub form a dense thorny scrubland around the lagoon, while the low thornscrub forms a discontinuous thorny landscape and is located to 0.6-0.7 km from the lagoon. Other three sites were located on dry uplands far from any water body (xeric sites – high water stress). These sites were defined as interrupted cactus thicket (Xeric 1), open cactus thicket (Xeric 2) and interrupted open cactus thicket (Xeric 3), which contain a high abundance of columnar cacti as well as high portions of open areas resulting in a xeric landscape strongly dominated by cacti. The xeric sites were separated from one another by approximately 10-12 km of distance. Field work was carried out from April to December, 2006.

3. Methods

3.1 Spatial assessment

We assessed the spatial association between columnar cacti and mimosoid shrubs' using eleven to twenty 50-m linear transects, which were randomly installed in each study site. This field sampling does not consider the isolated or clumped condition of perennial shrubs and therefore there is a direct relationship between plant cover and the number of columnar cacti recorded. In each transect, we counted all columnar cacti growing beneath mimosoid shrubs, other perennial plants and in open areas to obtain the observed frequencies and compare them with those expected under the hypothesis of random distribution. We considered all perennial plants with at least 50 cm height, including two cacti of prostrate-erect habit (*Opuntia caribea* Britton & Rose and *O. depauperata* Britton & Rose) and common medium-sized ephemeral plant species. We identified all the shrubs in each transect and obtained their diameter through foliage interception of focal plants along the transects. We estimated plant species cover assuming that all species had circular-shaped crowns. We used separate Chi-square tests ($\chi 2$) 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 plant species. We assessed the significance of each cell using standardized residuals tests. We assumed that the standardized residuals are normally distributed with a zero mean and unit variance, so that any value greater than 2 was regarded as a significant deviation.

3.2 Seed germination

Fresh fruits from 25-30 different individual cacti of *C. repandus* and *S. griseus* were gathered during their peak fruiting period (March-May, 2006). In laboratory conditions, the fruit pulp was offered to 4-8 individuals of *G. longirostris* to obtain cactus seeds passed through the intestinal tracts of their dispersers. Seeds were dried on absorbent paper before placing them into small plastic bags until experiments were carried out. The rate of seed germination beneath four different conditions of soil and two conditions of shade was evaluated through a field experiment. Soils were extracted from open spaces and under the crowns of *P. juliflora* growing in a mesic and a xeric site. The shading factor consisted of two conditions, namely as i) shade by the isolated canopy of a *Prosopis* shrub and ii) openings. The experimental unit for all treatments consisted of a plastic container in which 30 seeds were sown. A total of 12 replicates per treatment were used. The cactus seeds were watered every day until field capacity. Each 2-days we counted the number of germinated seeds per plastic container until

there was no further germination over a minimum of three consecutive days. The criterion used to consider a seed geminated was radicle emergence from the embryo. The germination experiments were performed under isolated shrubs of P. juliflora which naturally occur in the Carlos Viscano Botanical Garden of the Universidad de Los Andes, San Juan de Lagunillas, Mérida, Venezuela (8°30'37'' N, 71°21'10''W). The proportion of germinated seeds at the end of the experiment was analysed with a log-linear model. Differences between the model without any interactions and the model that includes all interactions were evaluated through marginal association tests with a 0.05 rejection level (Zar 1996) using the Statistica 6.0 package version.

To analyse the germination of cacti seeds, three additional parameters were took into consideration: (1) germination capacity (GC), which refers to the proportion of cactus seeds capable of germinating under an experimental condition, (2) minimum imbibition time (Tmi), which is the minimum required for the seeds to start germination once they have absorbed the necessary amount of water; and (3) time necessary for reaching 50% germination capacity (T50), which indicates the time necessary for germination of at least the half the seeds that had actually germinated at the end of the experiment (1/2GC).

3.3 Seedling survival

Seedling survival was assessed by performing an exclosure experiment with two treatments. For each site, seeds of *S. griseus* and *C. repandus* were sown in nursery pots filled with homogenized soil collected from open spaces and beneath the canopies of *P. juliflora*. All seedlings were obtained from seeds "treated by dispersers". The seeds were watered every two days until field capacity. The germination and early growth of seedlings was performed in the nursery of the Carlos Viscano Botanical Garden under ambient conditions of temperature (mean: 24.3°C, min: 17.9°C, max: 37.9°C) and relative humidity (mean: 76.9%, min: 29.2%, max: 98.9%). During the last seven days prior to being transported to the field, seedlings were acclimatized by decreasing watering. In each site, two groups of 20 seedlings about a month old were placed in a) beneath isolated shrubs of *P. juliflora* and b) open areas. In each mesohabitat, a group of 20 seedlings was placed exposed areas allowing free access to all potential predators of seedlings, while the second group was placed in exclosures preventing access by small vertebrates. Exclosures consisted of a 20 cm high square cage of metallic mesh with 0.4-mm openings, closed to top. Both treatments (control and exclosure for small vertebrates) were protected with a 40 cm high square cage of galvanized wire of 2.5-cm openings to prevent the trample by goats but allow access of small vertebrates to control treatment. All seedlings were numbered and planted with their nursery pots to facilitate their survivorship control.

In the xeric site, *S. griseus* seedlings were placed beneath eight isolated shrubs of *P. juliflora* and its matching open spaces, while *C. repandus* seedlings were planted underneath six focal shrubs and its corresponding open areas. In the mesic site, *S. griseus* seedlings were located beneath eight isolated shrubs of *P. juliflora* and open spaces, while *C. repandus* seedlings were only planted under three isolated individuals of *P. juliflora* and open areas. These differences were produced by the low amount of seedling that we obtained under nursery conditions. Even though the germination of both cacti species tend to be similar, the proportion of seedling that were able to arrive to a month old was low. This tendency was evident in those seeds sowed in the homogenized soil from mesic site. In each site, the number of surviving cactus seedlings was recorded about every 15 days by four months (June-September 2006).

4. Results

4.1 Spatial assessment

The area covered by the canopy of *P. juliflora* shrubs was relatively high in all mesic and xeric sites studied (13.8 [Mesic 1] – 54.5% [Xeric 1]; min – max). Moreover, the area covered by *A. macracantha* shrubs was high in both mesic sites, mainly in Mesic 1 (46.8%), whereas the area covered by *A. farnesiana* shrubs was relatively high in all xeric sites, mainly in Xeric 3 (35.1%).

We recorded other thorny legume species, such as *Acacia tortuosa* (Willd.) L., *Acacia tamarandifolia* (Willd.) L., *Cassia emarginata* L. and *Leucaena leucocephala* (Lam.) De Wit (exotic species), which we only found in the mesic sites. The proportion occupied by open areas was relatively low in both mesic sites (< 23%) and ranged from 32.6% to 75.6% in the xeric sites. Overall, we recorded on 50-m linear transects from 254 to 778 individuals of *S. griseus*, *C. repandus* and *P. tillianus*. Among these, *S. griseus* had a clumped pattern under *P. juliflora* in xeric sites.

We also found a positive spatial association between *S. griseus* and *P. juliflora* in one of the two mesic sites (Mesic 1), suggesting that positive effects of this mimosoid plant as a nurse plant could also be occurring in a habitat with relatively low water stress. We also recorded positive spatial associations between columnar cacti and *Capsicum frutescens* L., *Capparis odoratissima* Jacq., *Cassia emarginata* L., *Cordia curassavica* (Jacq.) Roem. & Schult., *Croton rhamnifolius* H.B.K. and *Jatropha gossypifolia* L. (see Tables 1-5). Many of these plant species appeared to modify the spatial distribution of *S. griseus*.

4.2 Seed germination

At the end of the experiment, we found a strong effect of shade on the rate of seed germination of both succulent plants. The proportion of germinated seeds from shade by the canopies of *Prosopis* shrubs was significantly greater than those in openings. Even though there was a tendency of higher rates of germination in our treatments with soil extracted from the xeric site, the effect of soil type was marginally significant, showing that shading by a nurse plant can be most important for the germination of both cacti seeds than soil type. For both cacti species, a high GC was found under shade conditions and in soil extracted from the xeric site (*S. griseus*: *ca.* 83%, *C. repandus*: *ca.* 67%); however, the effect of interaction between these abiotic variables was not significant. Seeds of both cacti species in all treatments germinated at 6-10 day, showing the Tmi was relatively similar in all conditions.

4.3 Seedling survival

Analysis of seedling survival showed that the effect of [1] site (xeric/mesic), [2] exclosure (control/exclosure for native vertebrates), [3] mesohabitat (undercanopy/open areas) and [4] cactus species were significant. Seedlings of both long-lived columnar cacti were alive in almost all treatments after 105 (*C. repandus*) – 135 (*S. griseus*) days of the beginning of the experiments.

In the mesic site, analysis of survivorship curves (Kaplan & Meier tests) for both species of columnar cacti indicated differences in the seedling survival between all treatments. Overall, 25% of all *S. griseus* seedlings died within the first 15 days of the experiment (160 seedlings) and 50% of these seedlings survived longer than 96 days (320 seedlings). In contrast, 25% of all *C. repandus* seedlings died in the first 13 day of the experiment (60 seedlings) and only 50% of these seedlings survived longer than 13 days (120). For both cactus species, the higher mortality of seedlings was found in the control treatment from open areas (*S. griseus*: 98.7%; *C. repandus*: 100%). The lower mortality of seedlings was recorded in the exclosures for small vertebrates underneath *P. juliflora* canopies (*S. griseus*: 20.6%; *C. repandus*: 56.7%).

In the xeric site, analysis of survivorship curves for both species of columnar cacti indicated differences in the seedling survival between all treatments. Overall, 25% of all *S. griseus* seedlings died within the first 54 days of the experiment (160 seedlings). In contrast, 25% of all *C. repandus* seedlings died in the first 13 day of the experiment (120 seedlings) and 50% of these seedlings survived longer than 84 days (240 seedlings). For both cactus species, the higher mortality of seedlings was found in the control treatment from open areas (*S. griseus*: 80.6%; *C. repandus*: 96.7%). The lower mortality of seedlings was recorded in the exclosures for small vertebrates underneath *P. juliflora* canopies (*S. griseus*: 7.5%; *C. repandus*: 15.8%).

Three manuscripts were prepared with data obtained; two of them were submitted to international scientific journals:

- Larrea-Alcázar DM, Soriano PS. Columnar cacti-shrub relationships in an Andean semiarid ecosystem in western Venezuela: xeric versus mesic habitats (submitted to Plant Ecology)
- Larrea-Alcázar DM, Murillo JJ, Figueredo CJ, Soriano PS. Globose cacti-mimosoid shrub spatial associations in a Venezuelan Andean dry valley (submitted to New Phytology)
- Larrea-Alcázar DM. Sexual establishment of two long-lived columnar cacti in an Andean semi-desert: when does the nurse plants matter? (in prep.)

5. Conclusions

According with our results, spatial associations between columnar cacti and mimosoid legumes and other perennial shrubs are relatively more frequent in the xeric (cactus thicket) than in mesic (thornscrub) sites. However, these cacti-shrub relationships are not restricted to these conditions and do not include all potentially interacting species.

Mimosoid legume and other potential benefactor plants found in these work, may be considered as key plant species for conservation and restoration strategies of this Andean semi-desert and the richness and endemism that it contains. Successful field tests in which seeds or cactus seedlings are placed close to these plants may demonstrate the potential of this approach.

The presence of cacti in open areas suggests that facilitation may be less important for establishment of columnar cacti species in this Andean semi-arid environment than in other arid zones, such as the Sonoran Desert, the Tehuacán Valley of the central Mexico and the Cardones National Park in Argentina.

Germination of both cacti in shady conditions was rapid, suggesting that survivors of seed predation may find underneath *P. juliflora* canopies favourable conditions to their germination. Seedling survival below *P. juliflora* shrubs was also higher than in open spaces. To our knowledge these are the first data from two columnar cacti growing in the Venezuelan Andes strongly supporting the occurrence of nurse plant phenomenon in these tropical zones.

Although our data support the occurrence of so-called nurse plant syndrome, likely, this is not unique mechanism that allows the natural regeneration of columnar cacti in the enclave. In both contrasting habitat (mesic vs. xeric), there is strong evidence of vegetative propagation of these succulent plants, which could explain the existence of juveniles and mature cacti in open spaces.

6. Budget:

£ 3,900 = $US 6,805; Rate of Exchange: £1.00 = $US 1.745 (March-April, 2006)

Item	Requested ($US)	Spent ($US)
Field equipment: - Digital Camera Sony DSC-P100 - Cameras Lorex CVC-6993P Day and Night Colour (*) - Monitor Coby 5" TFT LCD Color TFTV-505 (*) - Mini loupe Korns - Target Capt TV/FM Terminator PCI KWorld	1,003.38	1,078.75
Travel and living expenses: - Field assistantship - Vehicle regular maintenance and services - Meals and fuel	5,139.03	4,418.60
Laboratory Analysis: - Soil analysis	436.25	158.60
Other expenses: - Books, photocopies and expendable supplies.	226.85	1,092.22
Total	**6,805**	**6,748**

(*) These equipments were donated to the Laboratory of Animal Ecology-A of the University of Los Andes, Mérida, Venezuela (Received by Prof. Pascual Soriano)