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THE NURSE-PLANT EFFECT OF *PROSOPIS FLEXUOSA* D.C. (LEG-MIM) IN A DRY VALLEY OF THE BOLIVIAN ANDES

EFECTO NODRIZA DE *PROSOPIS FLEXUOSA* D.C. (LEG-MIN) EN UN VALLE SECO DE LOS ANDES BOLIVIANOS

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ABSTRACT

The role of *Prosopis flexuosa* D.C. (Leg-Mim) as a nurse plant for establishment of other plant species was evaluated in an Andean semiarid dry valley of Bolivia (Mecapaca, La Paz). It is the first study that evaluates possible plant-plant positive interactions in these xeric environments. Abundance and species richness under the crown of *P. flexuosa* were recorded and compared to those in open spaces lacking the influence of any kind of canopy. In all, 21 species between woody plants and big perennial herbs were recorded under the canopy of *P. flexuosa* (3-4 species/tree), while 17 species occurred in open areas (13 species were common to both; Sörensen index = 0.34). The abundance of three Asteraceae species: *Baccharis boliviensis*, *Viguiera australis* and *Verbesina cinerea* was significantly higher beneath the canopy of *P. flexuosa* than in open spaces, which suggests quantitative rather than qualitative benefits of *P. flexuosa* as a nurse plant. Moreover, individuals of *Corryocactus melanotrichus* (Cactaceae), *Dodonaea viscosa* (Sapindaceae) and *Krameria lappacea* (Krameriaceae) were more abundant outside than underneath shrubs, suggesting that these species can establish in open areas. We postulate that *P. flexuosa* may modify the spatial pattern of small shrubs affecting species replacement rather than species enrichment. We discuss how species replacement may contribute to increase the local diversity and, mainly, to a possible dynamic patch structure.

Key Words: abundance, benefactor plant, facilitation, floristic composition

RESUMEN

Evaluamos cuantitativamente la importancia de *Prosopis flexuosa* D.C. (Leg-Mim) como especie facilitadora para el establecimiento de otras especies de plantas en un valle seco semiárido de los Andes de Bolivia (Mecapaca, La Paz). Este es el primer estudio que analiza las interacciones positivas planta-planta en estos ambientes. La abundancia y la riqueza de especies fueron registradas bajo la copa de *P. flexuosa* y comparadas con aquellas que ocurren en espacios abiertos sin influencia de ningún tipo de sombra. En total, 21 especies entre plantas leñosas y herbáceas perennes se establecen bajo la copa de *P. flexuosa* (3-4 especies/árbol), mientras que 17 especies fueron registradas en zonas abiertas (13 especies fueron comunes para ambos hábitats, Índice de Sörensen = 0,34). La abundancia de tres especies de Asteraceae: *Baccharis boliviensis*, *Viguiera australis* y *Verbesina cinerea* fue significativamente mayor bajo la copa de *P. flexuosa* que en zonas abiertas, lo cual sugiere beneficios cuantitativos más que cualitativos de *P. flexuosa* como planta nodriza. Por el contrario, individuos de *Corryocactus melanotrichus* (Cactaceae), *Dodonaea viscosa* (Sapindaceae) y *Krameria lappacea* (Krameriaceae) fueron más abundantes lejos que bajo la copa de *P. flexuosa*, sugiriendo que estas especies son capaces de establecerse en espacios abiertos. Postulamos que *P. flexuosa* puede modificar los patrones espaciales de arbustos pequeños afectando el reemplazo de especies en lugar de la riqueza de especies. Discutimos cómo el reemplazo de especies puede contribuir a incrementar la diversidad local y principalmente a una posible dinámica de estructura de parches.

Palabras clave: abundancia, facilitación, composición florística, planta benefactora.

INTRODUCTION

Positive interactions between plants can determine community structure and local diversity in many habitats (Callaway 1995, Callaway and Walker 1997, Tewksbury and Lloyd 2001). One of such positive interactions is the so-called nurse plant association phenomenon, in which certain plants enhance the establishment of other plants (Bertness and Callaway 1994). The effect of the nurse plant depends on the size/age of the benefactor plant (Franco and Nobel 1989, Valiente-Banuet and Ezcurra 1991, Valiente-Banuet *et al*. 1991, Tewksbury *et al.* 1999). Habit seems to be also another important attribute, as evergreens and plants with dense crowns have been found to be better benefactors compared to other growth forms (Flores and Jurado 2003), because also they can produce "resource islands" under its crowns with high levels of nitrogen, phosphorous, organic matters and other soil elements (Pugnaire *et al.* 1996, Rossi and Villagra 2003). For these reasons, nurse plants influence the natural regeneration, growth, and spatial associations of the beneficiary plants (e.g., Dawson 1993, Tewksbury et al. 2001), and their canopy can foster the presence of a greater number of woody plants when compared to open spaces (Valiente-Banuet and Ezcurra 1991, Tewksbury *et al.* 1999).

Prosopis flexuosa is a 4-5 m tall, thorny mimosoid legume, which grows as a more or less sparsely distributed tree or shrub in the Andean dry valleys of Bolivia and Argentina. The Andean dry valleys of Bolivia are dominated by the plant families Compositae, Cactaceae, Gramineae, and Leguminosae, and by the genera *Tillandsia*, *Baccharis*, *Solanum*, and *Parodia* (López 2003). The genus *Prosopis*, with nine species, is very important in this biogeographical region, both by number of species and considering abundance (cover, density). Among all species of genus, *P. flexuosa* is an important element in these habitats because its canopy provides shade that could facilitate the establishment of other woody plants (*sensu* Vilela and Ravetta 2001). In fact, this species tend to be the dominant woody species in dry landscapes where they occur. The low abundance of conspecific seedlings under the crown of *P. flexuosa* could be due to high predation of its seeds by birds and rodents (Campos and Ojeda 1997, Villagra *et al*. 2002, Saba and Toyos 2003) and to their low viability (Urcullo 1996). This suggests that free spaces can be available under the crown of *P. flexuosa* for the arrival, survival and growth of heterospecific plants. Thus, this species would play the role of potential nurse plant influencing the natural regeneration dynamics in these habitats (Rossi and Villagra 2003, Valdivia 2005).

The objective of this work was to evaluate the establishment of woody plants under the canopy of *P. flexuosa* to compare it to the natural regeneration that occurs in open spaces lacking shade. We tried to answer the following two questions: 1) How many species are growing beneath *P. flexuosa* canopy? and 2) Can *P. flexuosa* shrubs affect the abundance of woody species and big perennial herbs growing under its canopy?. We evaluated the hypothesis that the trees of *P. flexuosa* can promote the biological diversity by modifying the richness and abundance of woody plants in these Andean dry valleys.

Study site

We chose a dry valley located 20 km to the southwest of the city of La Paz, Bolivia, at 2900 m asl. The study site, locally known as Mecapaca, is characterized by a warm climate with 17°C and a mean annual rainfall of 490 mm. The study was conducted at the beginning of the dry season (May 2003). The region is characterized by its mountainous character, with geomorphic unities that include river beds, floodplains as well as lateral gorges (Beck and Garcia 1991). In the past, the flora of these valleys was composed of *Schinopsis* and *Schinus* (Anacardiaceae), species of *Duranta* and *Citharexyllum* (Verbenaceae), *Jacaranda* and *Tecoma* (Bignoniaceae), and species of *Caesalpinia* and *Prosopis* (Beck and Garcia 1991). Today, they are dominated, in the less disturbed sites (which are indeed very few), by *P. flexuosa*, *Pluchea fastigiata*, *Baccharis boliviensis* and *Verbesina cinerea* (Asteraceae), as well as by *Dodonaea viscosa* (Sapindaceae), and different cactus species (R.P. López, personal observation). *P. flexuosa* is the dominant woody plant species of landscape, which make this semiarid environment distinct and appropriate to evaluate the importance of this mimosoid species as benefactor plant to establishment of other small-sized woody plants.

METHODS

P. flexuosa abundance was determined by twelve 50-m linear transects (total area = 0.12 ha),

recording, in each transect, the number of adult individuals (basal diameter, BD > 2.5 cm), juveniles (BD = 1.0 – 2.5 cm) and seedlings (BD < 1 cm). In order to assess the establishment of woody plants, we selected 20 *P. flexuosa* trees and shrubs approximately 3-4 m high and with a BD > 15 cm. We chose isolated individuals to avoid the influence of adjacent neighbors. In each case, natural regeneration both below (< 2 m radius) and away from the shrubs crown (> 2 m radius) was recorded through two 1 m^2 quadrats. The latter were open zones without the influence of other trees/shrubs' crowns. In each quadrat, all the woody species and perennial herbs was recorded, including number of individuals of each species. Botanical samples were collected and compared to collection specimens of the National Herbarium of Bolivia (LPB) to ascertain taxonomical identity. Differences in species richness and abundance were analyzed through t-tests for dependent samples. Differences in abundance for each species were evaluated through tests of differences between two proportions (z values). Statistica package (version 6.0) was used in both cases with a 0.05 rejection level.

RESULTS

We recorded 73 individuals of *P. flexuosa*, of which 36 were adults and 37 juveniles. No seedling was recorded on transects. Abundance of adult individuals (3.0 ± 0.35; mean ± SE) did not differ from that of juvenile individuals (3.1 ± 0.65)(t = -0.11, p = 0.91).

A total of 21 plant species were recorded under the canopy of *P. flexuosa*, while 17 species were recorded in open spaces. The species similarity between both microhabitats was relatively low (13 species in common, Sörensen Index= 0.34)(Table 1). Under the crown of *P. flexuosa*, we detected no seedlings of this species, but we found juveniles (1/40 quadrats for each treatment). The number of species under *P. flexuosa* canopy (3.4 ± 0.17, mean ± SE) did not differ from the number of species in open places (3.6 ± 0.22)(t = -0.71, p = 0.48)(Figure 1). In all, under *P. flexuosa*

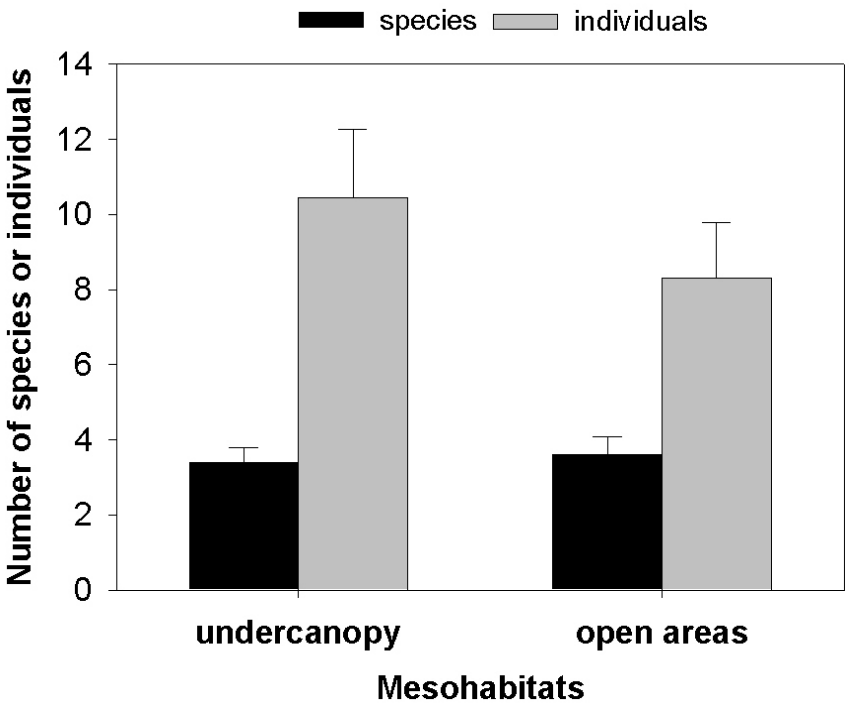

Figure 1. Number of species and abundance of individuals per plot under *Prosopis flexuosa* canopies and open areas in a dry valley in the Bolivian Andean. Bars represent mean values and vertical lines ±2SE.

we found 421 individuals (4-22, min-max/quadrat), whereas in open spots 332 individuals were recorded (2-18, min-max/quadrat). Differences in abundance of woody plants and big perennial herbs growing beneath canopy of *P. flexuosa* (10.5 ± 0.8) and open areas (8.3 ± 0.7) were statistically significant ($t = 2.53$, $p = 0.043$)(Figure 1).

The most abundant species of plants both underneath as well as far from *P. flexuosa's* canopy were *Baccharis boliviensis* (Asteraceae)(179 and 113 individuals, respectively) and *Lantana balansae* (Verbenaceae)(114 and 98 individuals, respectively)(Table 1). The less abundant species under *P. flexuosa* were *Iresine spiculigera* (Amaranthaceae), *Atriplex semibaccata* (Chenopodiaceae), *Wissadula andina* (Asteraceae), *Minthostachys* cf. *acutifolia* (Lamiaceae), *Solanum* sp. (Solanaceae) and *P. flexuosa*. In the areas adjacent to these plants, the less abundant species were *Tecoma arequipensis* (Bignoniaceae), *Stevia bangii* (Asteraceae), *Croton emporiorum* (Euphorbiaceae) and *Opuntia* sp. (Cactaceae). In both cases, we only found one individual in each of these species (Table 1). Of all of them, abundance of *B. boliviensis*, *Viguera australis* and *Verbesina cinerea* was significantly higher beneath the canopy of *P. flexuosa* than in open areas ($p < 0.05$, Table 1). In contrast, abundance of *Corryocactus melanotrichus* (Cactaceae), *Dodonaea viscosa* (Sapindaceae) and *Krameria lappacea* (Krameriaceae) was greater far from *P. flexuosa's* canopy than underneath these shrubs ($p < 0.05$, Table 1).

The species exclusively recorded under *P. flexuosa* were *Heliotropum microstachyum* (Boraginaceae), *Verbesina cinerea* y *Senecio* sp. (Asteraceae), as well as *M. acutifolia, Solanum* sp., *I. spiculigena, A. semibaccata* y *W. andina* (8/21 species). In contrast, the species occurring exclusively in open places were *K. lappacea* (Krameriaceae), *Salvia haenkei* (Lamiaceae), *T. arequipensis* y *S. bangii* (4/17 species).

DISCUSSION

Our results suggest that *P. flexuosa* shrubs can increase the abundance of small shrub species underneath its crown likely producing heterogeneity and spatial association at different scales. It seems that species richness is not greater under canopy cover as compared to open spaces, but as the composition between both sites differs, overall species richness increases. No difference of species richness underneath *P. flexuosa* than open areas also had been reported in the Monte Desert, Argentina (Rossi and Villagra 2003). Although 3-4 species, on average, were found below each tree of *P. flexuosa*, eight species occurred exclusively underneath the canopies of these shrubs, which hint to a qualitative consequence of the facilitator effect of these trees. Moreover, the abundant presence of heterospecific plants points to a reduced survival of conspecific seeds and/or seedlings, which is likely one of the causes of the establishment of individuals of other species; thus, generation of free spaces under the canopy of *P. flexuosa* may be the result of low natural regeneration of this species. In fact, seeds of *P. flexuosa* in the Monte Desert are severely consumed by different ants and one herbivorous hystricognath rodent, the mara (*Dolichotis pataganum*, Caviidae)(Campos and Ojeda 1997, Villagra *et al.* 2002). Besides, like other legume species, seeds of *P. flexuosa* may be strongly damaged by bruchids (Orozco-Almanza *et al*. 2003). Unfortunately, the pre- and postdispersal fate of seeds of this legume species in the Bolivian Andean dry valleys is unknown.

The species recorded have small seeds that are possibly dispersed by anemochory pathway. Presence of Cactaceae (species of the genera *Opuntia* and *Corryocactus*) could imply seed arrival via zoochory suggesting the potential use of *P. flexuosa* as perch sites by frugivorous birds that consumed these fleshy fruits. Positive associations between cacti and perennial shrubs have been reported in many arid and semiarid environments (Flores and Jurado 2003), although in other cases some species of columnar cacti may also play the role of nurses (Nobel and Bobich 2002). Our results suggest, at least for case of *C. melanotrichus*, that some cacti species may not require a benefactor plant for its establishment. If this occurs, relative high rates of vegetative propagation could explain the low abundance of these cacti under the canopy of *P. flexuosa* (Mandujano *et al.* 1996).

Tewksbury and Lloyd (2001) report that the effect of *Olneya tesota* as a nurse plant depends on the mesic or xeric sites where it grows. The effect of *P. flexuosa* as a nurse plant could vary depending on the zone where it grows. Thus, the influence of this legume species on beneficiary plants that grow under its canopy could change depending on the competitive effects that these

Table 1. Abundance of species registered beneath canopy of *Prosopis flexuosa* and open areas in a dry valley in the Bolivian Andean. Values represent the number of individuals (and %). Last column shows levels of significance of tests on differences between proportions underneath and outside shrubs for each species.

Family	Species	Undercanopy	Open Areas	p-level
Equisetaceae	*Ephedra americana*	8 (0.019)	5 (0.015)	0.676
Amaranthaceae	*Iresine spiculigena*	1 (0.002)	-	0.415
Asteraceae	*Baccharis boliviensis*	179 (0.425)	113 (0.340)	0.012
	Pluchea fastigiata	8 (0.019)	6 (0.018)	0.919
	Senecio sp.	2 (0.005)	-	0.197
	Stevia bangii	-	1 (0.003)	0.261
	Verbesina cinerea	5 (0.012)	-	0.046
	Viguiera australis	39 (0.093)	8 (0.024)	< 0.001
	Wissadula andina	1 (0.002)	-	0.415
Bignoniaceae	*Tecoma arequipensis*	-	1 (0.003)	0.261
Boraginaceae	*Heliotropium microstachyum*	2 (0.005)	-	0.197
Cactaceae	*Corryocactus melanotrichus*	24 (0.057)	41 (0.123)	0.004
	Opuntia sp.	4 (0.010)	1 (0.003)	0.250
Chenopodiaceae	*Atriplex rusbyi*	5 (0.012)	6 (0.018)	0.496
	Atriplex semibaccata	1(0.002)	-	0.415
Euphorbiaceae	*Croton emporiorum*	3 (0.007)	1 (0.003)	0.450
Krameriaceae	*Krameria lappacea*	-	9 (0.027)	0.001
Lamiaceae	*Salvia haenkei*	-	2 (0.006)	0.112
	Minthostachys cf. *acutifolia*	1 (0.002)	-	0.415
Leg-Mim	*Caesalpinia bangii*	9 (0.021)	6 (0.018)	0.769
	Prosopis flexuosa	1 (0.002)	3 (0.009)	0.180
Sapindaceae	*Dodonaea viscosa*	3 (0.007)	27 (0.081)	< 0.001
Scrophulariaceae	*Agalinis lanceolata*	10 (0.024)	4 (0.012)	0.272
Solanaceae	*Solanum* sp.	1 (0.002)	-	0.415
Verbenaceae	*Lantana balansae*	114 (0.271)	98 (0.340)	0.365
TOTAL		**421**	**332**	

plants create as they grow in benign conditions (mesic sites) and on those mechanisms that prevent the arrival of new individuals (*sensu* Suzán *et al.* 1996, Tewksbury *et al.* 1999, Tewksbury and Lloyd 2001). For example, *Viguiera australis* was more abundant underneath *P. flexuosa* than in open spaces, probably due to the fact that this species might have accumulated more seeds than in the open. Thus, the change in floristic composition could imply the replacement of species according to life form since small shrubs were best represented in the *P. flexuosa* understory (*sensu* Rossi and

Villagra 2003). As in other semiarid landscape, the higher plant abundance under *P. flexuosa* may be due to the fact that these shrubs could create fertility islands under its canopy. In fact, high N concentration has been found under *P. flexuosa* shrubs growing in Mecapaca than in open areas (0.75% and 0.09%, respectively)(Valdivia 2005) showing that these dominant woody plants are capable causing change in soil properties under their crown and favour the presence of small species.

On the other hand, other species could also have the capacity of functioning as nurses. Since it seems to show a correlation between the size of the benefactor plant and the number of plants that are recruited beneath its crown (Haase *et al.* 1996, Callaway and Walker 1997), it would be expected that other big shrubs of the region could play the role of nurse plants. In this respect, *Pluchea fastigiata* and *Dodonaea viscosa* could be mentioned. These are shrubs that can reach 2 m in height and which are also abundant in the study region. Nevertheless, one small but abundant species, *Baccharis boliviensis*, appears to behave as a nurse plant too (R.P. López, personal observation). This is different from the role this species has in a more arid, though somehow related, Andean semi-desert of northern Argentina, the Prepuna, where *B. boliviensis* has negative effects on other species, apparently due to the allelochemicals it contains (de Viana *et al.* 2001).

In summary, our data suggest the *P. flexuosa* shrubs can influence the abundance of some species and the floristic composition of the plants that grow underneath it. Although species richness is not greater under its canopy (vs. open spaces), by allowing different species to survive below its crown, *P. flexuosa* can increase the species richness of these Andean valleys. The results of its benefits as a benefactor plant should be reflected in the survival and reproduction of these species, aspects that were not assessed in this study, but should be part of future researches.

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