

Effect of *Prosopis flexuosa* on understory species and its importance to pastoral management in woodlands of the Central Monte Desert *

Efecto de *Prosopis flexuosa* sobre las especies del sotobosque y su importancia para el manejo pastoril de los algarrobales del desierto del Monte Central

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Originales: Recepción: 28/10/2011 - Aceptación: 09/10/2012

ABSTRACT

In the Monte Biogeographic Province, located in the arid region of Argentina, the presence of *Prosopis flexuosa* DC. produces spatial heterogeneity through edaphic modifications and microclimate changes. This results in vegetation patches differing in species composition and abundance. However, this interaction can be modified by the occurrence of gradients of biotic stress or disturbance intensity. In particular, grazing has been observed to enhance or reduce vegetation heterogeneity. Such complex of interactions could determine forage availability for cattle in one of the driest areas of the Monte Desert. We assessed the effect of *Prosopis* on understory species and analyzed whether the outcomes of this interaction differed with distance to watering points, as a proxy of grazing intensity, in the Northeast of Mendoza Province, Argentina. We used a two-way factorial design including the following factors: 1) microsite (under the cover of *P. flexuosa* trees and in intercanopy microsites) and 2) distance to watering points ("near the watering point", 500-700 m away, and "far from the watering point", 3-4 km away). Cover of each species,

RESUMEN

En la Provincia Biogeográfica del Monte, ubicada en la zona árida de Argentina, la presencia de *Prosopis flexuosa* DC. genera heterogeneidad espacial a través de modificaciones edáficas y cambios microclimáticos, lo que genera parches de vegetación con distinta composición florística y abundancia de especies. Sin embargo, esta interacción puede ser modificada por la presencia de gradientes de estrés biótico o de intensidad de disturbio. En particular, se ha observado que el pastoreo puede incrementar o disminuir la heterogeneidad espacial. Este complejo de interacciones puede determinar la disponibilidad de forraje en una de las zonas más áridas del Monte. Este estudio analiza la influencia de *P. flexuosa* sobre el patrón espacial del resto de las especies de la comunidad y cómo esta interacción es modificada según la distancia a la aguada, tomada como un indicador de la intensidad de pastoreo, en el Noreste de la Provincia de Mendoza, Argentina. Fue realizado un diseño bifactorial, incluyendo los siguientes factores: 1) micrositio ("bajo la cobertura de *P. flexuosa*" y "áreas expuestas") y

* This study was supported by Agencia Nacional de Promoción Científica y Tecnológica (Argentina) (PICT 2007 01222) and Universidad Nacional de Cuyo.

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total cover, bare soil, and litter were recorded, and plant diversity, richness, and evenness were estimated with the modified Point Quadrat method. Results showed that *P. flexuosa* cover, distance from watering points, and the interaction between them determined species composition, abundance and spatial distribution of understory species, and were, consequently, a determining factor for forage availability. The presence of *P. flexuosa* enhances carrying capacity by supporting higher abundance of grasses under its canopy. Near watering points, high grazing intensity appears to disrupt the patches formed under *P. flexuosa* canopies, reducing the differences between microsites.

2) distancia a la aguada ("cerca de la aguada", desde 500 hasta 700 m, y "lejos de la aguada", entre 3 y 4 km). Se registró la cobertura de cada especie, cobertura total, suelo desnudo y mantillo, y se estimó la diversidad, riqueza y equitatividad a través del método de Point Quadrat modificado. Los resultados muestran que la cobertura de *P. flexuosa*, la distancia a la aguada y la interacción entre ambas determinan la composición, abundancia y distribución espacial de las especies en la comunidad y, consecuentemente, la disponibilidad de forraje. La presencia de *P. flexuosa* aumenta la capacidad de carga incrementando la abundancia de pastos bajo su dosel, aportando por lo tanto a la cobertura forrajera. Cerca de la aguada, la alta intensidad ganadera disminuye el efecto de *P. flexuosa* al disminuir la diferencia entre los micrositios.

Keywords

spatial heterogeneity • patchiness • facilitation • distance from watering points • forage availability

Palabras clave

heterogeneidad espacial • parches • facilitación • distancia a la aguada • disponibilidad de forraje

INTRODUCTION

In arid and semiarid environments, with scarce and patchy plant cover, it is usual to observe vegetation growing mostly around trees and shrubs (3, 13). Woody plants can have positive, negative or neutral effects on other species (21, 44, 51). Tree cover influences the likelihood of seedling establishment in woodlands by modifying physical environmental conditions (8, 9, 44). Some species are able to increase local soil fertility through accumulation of carbon and nitrogen and modification of the decomposition rate (34, 42, 56); through increased infiltration rate (29, 44), and through protection against high temperatures and radiation (16, 29, 44).

Thus, it has been proposed that positive interactions among plants are an essential mechanism to maintain diversity at regional scale (29, 33, 52, 53). However, the presence of woody plants can also negatively influence other species through light reduction, allelopathy, or certain mechanical and chemical effects caused by litter (22) and, in environments where water is the major limiting factor, there may be competition for water and nutrients (18).

The final effect of environmental changes produced by woody species on the spatial pattern of the plant community depends on the different environmental requirements of each understory species and on its ability to adjust to such changes. Therefore, the effect of the presence of woody species on the community is the

result of the balance between positive (facilitation) and negative effects (competition, inhibition) on the different species (10, 17, 44, 51). This balance may change for each species according to physical environmental conditions. Positive interactions seem to be more important with higher abiotic stress, whereas negative interactions, such as competition, seem to be dominant when abiotic stress is relatively low (10, 44). However, this relation seems to be modified by the occurrence of gradients in biotic stress or disturbance intensity, e. g. increasing grazing pressure (52). The pattern of disturbance can interact with other causes of heterogeneity and alter vegetation patchiness (10, 43) or change its scale of expression (2, 11, 47). This interaction has strong consequences in the functional processes of ecosystems and, therefore, in their potential management. In particular, grazing has been observed to enhance or reduce vegetation heterogeneity by modifying water and nutrient cycles (2, 12), by affecting the facilitative capacity of woody plants through reduction of their crowns (52) or by fragmentation of large shrub clumps into smaller units and differential use of microsites (41). However, the final effect of grazing on positive plant interactions depends on grazing intensity, on the palatability of interacting species, and on the mechanisms involved in plant-plant interactions (47).

Herbivores select their food according to palatability of the plant species, and therefore species can be classified into preferred, indifferent or avoided (7). Overgrazing decreases the proportion of highly palatable species, increasing the proportion of grazing-tolerant and invading species (50). However, the presence of tolerant species can act as physical protection for preferred species, thereby contributing to their persistence (47). In addition, the grazing effect includes other action mechanisms such as trampling and fruit dispersal.

The Monte Biogeographic Province occupies a large expanse of the arid region of western Argentina (14). The major activity carried out in the Monte is extensive livestock production, particularly goat breeding (55). *Prosopis flexuosa* DC. is the main tree species and, because of the capacity of its roots to reach the water table, it forms woodlands in areas where groundwater occurs (30, 54), and is a major contributor to community structure. The edaphic and microclimatic changes caused by this species cover produce spatial heterogeneity and, consequently, modify species distribution (5, 45). Studies have been conducted on the effect of grazing on vegetation structure (23, 38, 39), on diversity and abundance of annual plants (48) and on the distribution of grasses in response to grazing gradients (27). However, the relation between spatial heterogeneity and disturbance is not yet well understood. In particular, the effects of grazing on the patchy pattern produced by woody species have been scarcely analyzed in the Monte Desert. In the Southern Monte, it has been observed that, besides reducing plant cover, grazing by domestic livestock can affect the structure and dynamics of vegetation patches by preventing litter accumulation or mineralization of organic matter (11, 12).

Therefore we hypothesized that the interaction between the facilitative effects of *Prosopis flexuosa* and grazing determine the composition, abundance, and spatial distribution of species in the community and, consequently, forage availability for cattle. The postulated mechanisms were: a) the facilitation by *P. flexuosa* determine the growth of vegetation mostly under its canopy; b) grazing reduce plant cover and

richness through the differential consumes of species in function of their palatability; c) grazing modify the structure of vegetation patches generated by the presence of *P. flexuosa* through the reduction of the facilitative capacity of this species and/or the differential use of each microsite.

Typically, grazing intensity and its environmental effects decrease as distance to the watering point increases (11, 12, 50). Therefore, the distance to the watering point can be used as a good surrogate of grazing intensity in studying the effect of grazing on plant interactions. In this work, we assessed the effect of *Prosopis* on understory species and analyzed whether the outcomes of this interaction differed with distance to watering points. We expected an increased difference between microsites near watering points in vegetation structure and richness if the prevalent mechanism is the differential uses of microsites by cattle, or a reduced difference if the lost of the facilitative capacity of *P. flexuosa* is the prevalent mechanism.

MATERIALS AND METHODS

Study area

The study area is located in the Northeast of Mendoza Province and includes 20,700 ha in the Telteca Reserve and surrounding areas. The study area lies entirely within the Monte Biogeographic Province, which is characterized by shrub steppe dominated by species of the family Zygophyllaceae (*Larrea* spp. and *Bulnesia retama*) and, in areas with higher water availability, by woodland of *P. flexuosa* (35, 46). The zone has a wide daily and annual temperature range; the absolute maximum temperature is 50°C and the absolute minimum is -10°C. Annual precipitation varies between 50 and 200 mm, with an average of 120 mm. The landforms of the area are predominantly aeolian, with sand dunes up to 20 m high (1). The *Prosopis* woodland is the community with highest carrying capacity (0.6-1.4 goat unit.ha⁻¹), which is several times higher than in *Larrea divaricata* shrubland or sand-dune communities (0.1-0.4 GU ha⁻¹) (6). We set up sampling plots in homogeneous areas of the most representative *P. flexuosa* woodlands. Mean density of this woodland is 207 individuals ha⁻¹, and the modal height of adult trees is between 4 and 6 m, modal basal diameter classes are between 15 and 25 cm, and modal crown diameter is between 5 and 6 m (4).

Experiment design

We used a two-way factorial design with microsites and distance from livestock watering points as factors. Two different microsites were considered: 1) under *P. flexuosa* canopy (under-*Prosopis* microsites) and 2) in areas outside the influence of this species (intercanopy microsites). Because the concentric effect of grazing around watering points reaches a 2 km radius (23), two levels were considered for the second factor: 1) 500-700 m from the watering point (referred to as "near the watering point") with high grazing pressure; and 2) 3-4 km from the watering point (referred to as "far from the watering point") with low grazing pressure. In the study area, watering points consist of different types of wells dug by local people to extract water for their livestock. Within the homogeneous areas, we chose the watering points of two typical settlements:

Los Rosales (32°17'S; 67°55'W) and El Jagüel (32°23' S; 67°58' W). These watering points were far enough from each other to allow us to set up sampling plots on the "far from the watering point" sites in areas without influence from any other watering point. In all, twelve sampling sites were selected at random: seven near watering points and five far from watering points. At each site, five trees representative of the most common classes (15-25 cm basal diameter, 4-6 m height, and 4-6 m crown diameter) were randomly selected. Five intercanopy microsites were selected 5-10 m away from the tree canopy to make sure they were outside the influence of the tree. The sampling technique used was the Modified Point Quadrat method (20, 37). On under-*Prosopis* microsites, the sample unit consisted of two transects of 50 points, set 4 cm apart. Each transect was set up at 1.5 m from the trunk, one in the Northern part of the canopy and the other in the southern part. Because intercanopy microsites are more extended and heterogeneous than under-*Prosopis* microsites, the sample unit consisted of two transects of 100 points, set 4 cm apart. Sampling was performed in May 2002 and in February 2003. No significant differences between dates were found ($P > 0.05$), so we considered both dates as the same data population.

Floristic composition, cover of each species, and percentage of bare soil and of litter-covered soil was recorded. Species richness was estimated as the number of species present at each site, and total plant cover was estimated as the percentage of points where at least one species was found. We estimated diversity and evenness using the Shannon index (31).

Species were classified into the following growth-forms that are present in the area: trees (phanerophytes more than 3 m tall and stems reaching 10 cm in basal diameter), shrubs (phanerophytes less than 3 m tall and several stems less than 5 cm in basal diameter), perennial grasses (hemicryptophytic grasses), annual grasses (therophytic grasses), forbs (non grassy hemicryptophytes and therophytes), and vines (creepers). We estimated cover and richness for the most abundant life forms: hemicryptophytic grasses, therophytic grasses and shrubs. In addition, we estimated fodder cover as the percentage of points where we found at least one fodder plant species. We defined fodder species in function of their specific quality index estimated in previous studies taking into account the acceptability, growth form, season of consumption, and nutritional value of each species (28, 36).

We considered each sampling site as only one entry representing a replication, and we considered the mean value of all five sampling units at each microsite.

Data analysis

Data were subjected to a two-factor analysis of variance. As the design was unbalanced, type III sum of square was used to test the hypothesis. When interactions between factors were significant, we used an a-posteriori mean comparison test (Tukey test) to compare pairs of the four possible treatment combinations (57). Because the data on species cover did not fit the assumptions of the variance analysis, they were transformed using rank transformations (19).

RESULTS

Under-*Prosopis* microsites showed a higher percentage of total cover (independent of the tree cover) and a lower percentage of bare soil than intercanopy microsites. The difference in the percentage of total cover between microsites seemed to increase in areas far from watering points, but interaction between microsite and distance from watering points was only marginally significant. The percentage of litter-covered soil was higher on under-*Prosopis* microsites than on intercanopy microsites, and it was similar for distance to watering points. Species richness and diversity were significantly greater far from watering points than near them, but there was no difference between microsites (table 1).

Table 1. Plant community parameters on the two microsites in relation to distance to watering points.

Tabla 1. Parámetros de la comunidad de plantas en dos micrositos en relación con las distancias a la aguada.

	Near watering point		Far from watering point		ANOVA (P)		
	Under canopy	Intercanopy areas	Under canopy	Intercanopy areas	M	WP	MxWP
Total cover	34 (7.8)	29 (10.9)	55 (10.7)	35 (6)	0.003	0.002	0.058
Richness	10.1 (3.2)	11.4 (3.4)	15.6 (3.7)	14.8 (3.6)	0.866	0.006	0.473
Diversity	1.9 (0.31)	2 (0.33)	2.3 (0.34)	2.3 (0.18)	0.655	0.015	0.668
Equitability	0.83 (0.04)	0.85 (0.03)	0.83 (0.05)	0.82 (0.06)	0.589	0.609	0.556
Bare soil	43 (9.3)	68.1 (9.6)	24.2 (10.5)	61.5 (4.9)	<0.0001	0.003	0.118
Litter	42.7 (9.9)	10.1 (2.9)	43 (10.4)	15 (6.5)	<0.0001	0.433	0.486

Data represent the mean (standard deviation). M = effect of microsite, WP = effect of distance to watering points and MxWP = interaction between M and WP.

Los datos representan la media (desvío estándar). M = efecto de micrositio, WP = efecto de la distancia a la aguada y MxWP = interacción entre M y WP.

Both microsite and distance to watering points affected floristic composition and relative abundance of species (table 2, page 213).

Some species occurred preferentially on under-*P. flexuosa* microsites, such as *Aristida mendocina*, *Pappophorum caespitosum* (only far from watering points), *Trichloris crinita*, and *Capparis atamisquea*. Other species showed preference for intercanopy microsites, such as *Tricomaria usillo* and *Sporobolus phleoides* (table 2, page 213). In turn, we were able to detect species that were indicative of stocking rates. For example, some species grew exclusively or preferentially far from watering points, such as *Eragrostis cilianensis*, *Aristida adscencionis*, *Ximena americana*, *Senna aphylla*, *Plectrocarpa tetracantha* (only in intercanopy microsites), *Aristida mendocina*, *Pappophorum caespitosum*, *Setaria leucopila*, and *Larrea divaricata*. In contrast, *Lycium tenuispinosum* occurred preferentially near watering points (table 2, page 213). Most species preferring sites far from watering points showed high specific quality index, except *Larrea divaricata* (table 2, page 213).

Table 2. Floristic and growth-form composition and percent cover of each species for the two distances to watering points and the two microsites.
Tabla 2. Composición florística y porcentajes de cobertura por forma de vida y especie para dos distancias a la aguada y dos micrositios.

	Near watering point		Far from watering point		ANOVA (P)		Specific quality index
	Under canopy	Intercanopy areas	Under canopy	Intercanopy areas	M	WP	
Therophytic Grasses							
<i>Aristida adscensionis</i>	0.4 (0.9)	0.3 (0.16)	5.6 (7.4)	2.5 (2.7)	0.29	0.02	0.33
	0	0	2 (3.1)	0.24 (0.3)	0.81	0.0017	0.81
<i>Bouteloua barbata</i>	0	0.05 (0.15)	1.9 (2.2)	1.5 (1.6)	0.51	0.0003	0.98
<i>Bouteloua aristidoides</i>	0.4 (0.9)	0.14 (0.2)	0.56 (1.2)	0.4 (0.9)	0.61	0.87	0.99
<i>Eragrostis cilianensis</i>	0	0	1.2 (1.9)	0.3 (0.7)	0.16	0.007	0.16
<i>Sporobolus phleoides</i>	0	0.08 (0.1)	0	0.08 (0.1)	0.03	0.77	0.77
Hemicryptophytic Grasses							
<i>Aristida mendocina</i>	10.6 (5.2)	4.4 (4.3)	26.0 (7.3)	8.8 (3.4)	<0.0001	0.0002	0.01
	2.6 (3.2)	0.9 (1.1)	7.8 (3.9)	3.6 (2.2)	0.05	0.0026	0.58
<i>Pappophorum caespitosum</i>	0.05 (0.15)	0.15 (0.3)	4.2 (3.1)	0.78 (0.8)	0.12	<0.0001	0.01
<i>Setaria leucopila</i>	1.1 (1.2)	0.82 (0.8)	6.6 (4.9)	2.1 (1.8)	0.12	0.01	0.33
<i>Sporobolus rigens</i>	2.1 (3.6)	1.4 (2.5)	0.2 (0.3)	1.5 (1.9)	0.46	0.83	0.61
<i>Trichloris crinita</i>	4.8 (3.2)	1.1 (1.6)	7.2 (4.3)	0.78 (0.9)	<0.0001	0.73	0.34
Shrubs							
<i>Atriplex lampa</i>	4.4 (4.5)	6 (2.9)	3.4 (5)	4 (3.1)	0.22	0.32	0.99
<i>Allenrolfea vaginata</i>	0.7 (2)	0.5 (1.4)	0	0	0.96	0.25	0.96
<i>Bougainvillea spinosa</i>	0.6 (1)	2 (1.6)	0.9 (0.8)	0.8 (1)	0.18	0.73	0.24
<i>Capparis atamisquea</i>	5.6 (4.7)	0.6 (0.9)	5.4 (6)	2.9 (1.8)	0.03	0.22	0.08
<i>Lycium chilense</i>	0.1 (0.2)	0.3 (0.4)	0.4 (0.3)	0.02 (0.04)	0.17	0.92	0.07
<i>Lycium tenuispinosum</i>	4 (4.2)	4.5 (1.2)	2.7 (4.8)	2.6 (3)	0.28	0.08	0.77
<i>Larrea divaricata</i>	0.4 (1.2)	0.4 (0.8)	1.4 (3.1)	2.5 (2.5)	0.19	0.04	0.40
<i>Plectrocarpa tetraacantha</i>	0	0	0	0.04 (0.08)	0.24	0.24	0.24
<i>Suaeda divaricata</i>	3 (2.2)	3.6 (2.8)	3.6 (2.5)	3.6 (2.6)	0.84	0.76	0.92
<i>Senna aphylla</i>	0	0	0.4 (0.9)	0.4 (0.8)	0.53	0.03	0.53
<i>Tricomaria usillo</i>	1.7 (2.4)	4.4 (3.4)	2 (2.5)	5 (4.2)	0.02	0.59	0.98
<i>Ximenesia americana</i>	0	0	0.5 (1)	0.1 (0.2)	0.94	0.10	0.94
Trees							
<i>Bulnesia retama</i>	2.2 (3.8)	1.8 (2.6)	2.4 (1.7)	1.2 (1.3)	0.45	0.83	0.74
	2.1 (3.8)	1.7 (2.6)	1.7 (1.5)	0.7 (0.9)	0.52	0.95	0.29
<i>Geoffroea decorticans</i>	0.08 (0.2)	0.03 (0.07)	0.3 (0.3)	0.5 (0.5)	0.82	0.01	0.66
<i>Prosopis flexuosa</i> (renewals)	0.03 (0.07)	0.03 (0.07)	0.4 (0.4)	0	0.006	0.04	0.006
<i>Forbs</i>	0	0	0.08 (0.2)	0.2 (0.4)	0.45	0.03	0.45
<i>Gomphrena mendocina</i>	0	0	0.08 (0.2)	0.2 (0.4)	0.45	0.03	0.45
<i>Vines</i>	0.1 (0.1)	0.08 (0.1)	0.2 (0.3)	0.02 (0.04)	0.069	0.94	0.46
<i>Tweedia brunonis</i>	0.1 (0.1)	0.08 (0.1)	0.2 (0.3)	0.02 (0.04)	0.069	0.94	0.46

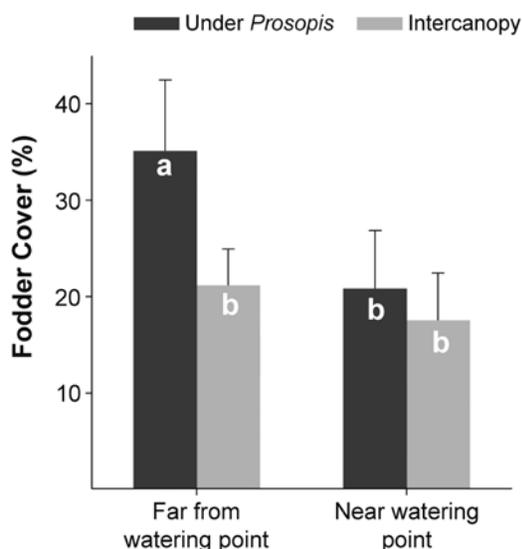
Data represent the mean (standard deviation). M = effect of microsite, WP = effect of distance to watering points, and MxWP = interaction between M and WP. The last column shows the specific quality index of the species analyzed according to Passera *et al.* (37).

Los datos representan la media (desvío estándar). M = efecto de micrositio, WP = efecto de la distancia a la aguada y MxWP = interacción entre M y WP. La última columna muestra el índice de calidad específico de las especies analizadas según Passera *et al.* (37).

The interaction between microsite and distance to watering points was significant only for *Pappophorum caespitosum* and *Prosopis flexuosa* (renewals), although *Capparis atamisquea* and *Lycium chilense* showed marginally significant probability values (table 1, page 212).

With respect to functional groups, hemicryptophytic grasses showed higher cover on under-*Prosopis* than intercanopy microsites, with this difference increasing far from watering points (interaction between microsite and distance to the watering point was significant) (table 2, page 213). Therophytic grasses showed a higher percentage of cover and richness on sites far from watering points, and showed no significant differences between microsites. No significant differences were observed for shrubs, either between microsites or between distances from watering sites.

Percent cover of fodder plant species was higher on under-*Prosopis* microsites than on intercanopy microsites (figure). The difference in cover between these two microsites was greater in areas far from watering points (interaction between microsite and distance to the watering point was significant).



Bars represent the mean, and vertical lines represent the standard deviation. ANOVA results: effect of microsite, $P = 0.001$; effect of distance to watering point, $P = 0.001$; interaction between microsite and distance to watering points, $P = 0.03$. Different letters in each treatment combination indicate significant differences at $P < 0.05$.

Las barras representan la media y las líneas verticales el desvío estándar. Resultados del ANOVA: efecto del micrositio, $P = 0,001$; efecto de la distancia a la aguada, $P = 0,001$; interacción micrositio y distancia a la aguada, $P = 0,03$. Letras distintas en cada combinación de tratamiento indican diferencias significativas en $P < 0,05$.

Figure. Effect of the cover of *Prosopis flexuosa* on forage cover in relation to distance to watering points and microsites.

Figura. Efecto de la cobertura de *Prosopis flexuosa* sobre la cobertura forrajera en relación con las distancias a la aguada y los micrositios.

DISCUSSION

In accordance with the postulated hypothesis, both the presence of *P. flexuosa* and grazing determined the composition and structure of plant associations in the Central Monte. *Prosopis flexuosa* modified the spatial pattern of associated species by generating vegetation patches with different floristic composition and relative abundance of their component species. However, no differences between microsites were found in richness and diversity. Besides, distance to the watering point also affected species abundance and composition, as well as the patch structure generated by *P. flexuosa*. We found some evidence indicating an interaction between both factors studied, which suggests that grazing alters the structure of vegetation patches produced by the cover of *P. flexuosa*. In general we observed that, near watering points, patch structure under *Prosopis* cover was disrupted and became more similar to that in intercanopy areas. This evidence supports Saiz & Alados proposals (47) suggesting a decreased association among species under high grazing intensity because of the lower protection effectiveness. Nevertheless, given that such evidence was true for only some of the studied variables, new research is needed to broaden our understanding of this relationship.

Because species richness and diversity were not affected by *P. flexuosa* cover, we attributed the change in floristic composition induced by *P. flexuosa* to species replacement. This is consistent with previous observations for Ñacuñán, a more humid area in the Monte (45). However, a higher percent of total cover under the canopy of *P. flexuosa* than in intercanopy microsites was found in Telteca, whereas no differences were found in total plant cover between both microsites in Ñacuñán (45). These results seem to indicate that the contribution of *P. flexuosa* to the productivity of understory species is higher in Telteca than in Ñacuñán. In addition, hemicryptophytic grasses occurred preferentially under the canopy of *P. flexuosa* in Telteca. On the other hand, it was observed that the same species occur preferentially in intercanopy microsites in Ñacuñán (45). Considering the higher water deficit in Telteca, the difference between both sites appears to support the stress-gradient hypothesis, which predicts that positive biological interactions become more important in relation to negative interactions when environmental stress increases (10, 43, 44). At this point, it is necessary to clarify that Ñacuñán is a natural reserve excluded from grazing and, therefore, could be an additional conditioning factor affecting the spatial distribution of grasses (40).

No differences were found between microsites or between distances to the watering point in total shrub cover, but species replacement was apparent, with some species, such as *Capparis atamisquea*, preferring under-*Prosopis* microsites, and other species, such as *Tricomaria usillo*, preferring intercanopy microsites. In arid zones, forage shrubs are key elements in livestock feeding (7), representing 35% of total forage intake and over 50% (of it) during the critical period of fodder shortage in the dry season (26). The species replacement that we observed may be important because of the resulting increased variability in the diet of livestock. In arid zones, availability of each species is variable depending on season. In the NE of Mendoza, in the autumn, at least 13 species were available for consumption by goats, whereas only nine were available in the winter (7).

In areas near watering points we observed higher proportion of bare soil and lower total cover, in addition to lower number of species and lower cover of hemicryptophytic and therophytic grasses. Thus, our findings concur with other studies for the Monte (11, 25) and other arid lands (50). Most of the species with a preference for areas far from watering points were grasses with a high specific quality index and a high degree of selectivity, such as *Pappophorum caespitosum*, *Setaria leucopila* or *Eragrostis cilianensis*. In contrast, *Lycium tenuispinosum*, with a preference for areas near watering points, shows the lowest specific quality index. In addition, the total percent cover of fodder species was lower near watering points. These findings suggest that intake by cattle is the main mechanism involved in the effect of grazing on vegetation structure as has been proposed by previous studies (27, 50). However, the decrease in the cover of *Larrea divaricata*, *Geoffroea decorticans* and *Senna aphylla*, species with the lowest specific quality index, suggests that other mechanisms, like trampling, should be involved in limiting the establishment or increasing the mortality of young plants in the area near watering points.

Several authors suggest that grazing affects interspecific interactions by modifying patch structure (2, 10, 11, 43, 47, 52). One of the most notorious effects of woody plants is the protection against herbivores they provide to fodder species, which is why, on grazed sites, it is usual for fodder species to show a denser distribution in vegetation patches, enhancing vegetation heterogeneity. As a result, in the most grazed areas, the most palatable species tend to group together under shrubs (15, 40, 47, 49). In this study, we found that the increase in grazing intensity reduces heterogeneity by reducing the differences between both microsites. This finding suggests that *P. flexuosa*, a tree with a more open growth form than shrubs, does not provide an effective barrier against goat grazing and trampling, at least on sites with high grazing intensity, and that the facilitating effect on fodder species is mainly a result of the edaphic and/or microclimate changes under the canopy.

The environmental heterogeneity created by *P. flexuosa* and the consequent facilitation effect on fodder species could explain the high stock carrying capacity observed in *Prosopis* woodlands (0.63-1.33 goat unit ha⁻¹) compared to the other communities in the region (6) and with that estimated by Guevara *et al.* (24) for the area (0.1 GU ha⁻¹) using data on rainfall use efficiency (32). This explanation is consistent with the proposal that heterogeneous vegetation in arid lands is more productive than homogeneous systems (3).

We can conclude that the carrying capacity of woodlands is enhanced by the presence of *P. flexuosa*, which provides a greater abundance of grasses under its canopy and, therefore, contributes to an increased forage cover. This concept is reinforced by the fact that the tree itself represents a major fodder contribution in the form of fruit and litter (7), a contribution that was not considered in this study. This conclusion suggests that recovery of degraded areas in the region through afforestation with *Prosopis* trees can yield benefits in terms of silvopastoral management. Therefore, our results contribute not only from a theoretical point of view to understanding the functional aspects of spatial heterogeneity and its relationship with disturbance, but also from a practical point of view to understanding the connections between two important activities in the economy of arid lands of the world, extensive grazing and the use of forest products.

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Acknowledgements

We thank José A. Boninsegna, Ricardo Villalba, and Alejandro Bisigato for their valuable suggestions.

We thank Gualberto Zalazar, Germán Berra, and Belén Lana for their cooperation in the field work.

We thank Nelly Horak and Judy Boshoven for improving the English version of the manuscript.