

Abundance and spatial patterning of coexisting perennial grasses in grazed shrublands of the Patagonian Monte

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Abstract

We analysed the density, bunch size, and spatial patterning in relation to the shrubby matrix of the three dominant perennial grasses of the Patagonian Monte with different functional traits related to resource acquisition/conservation, mesophytism/xerophytism, and reproductive strategy. Field sampling was carried out at grazed (low and high grazing pressure) and excluded from grazing (15 years) sites. Grazing disturbance did not change the cover of the shrubby matrix but modified its spatial structure leading to increased density and reduced diameter of shrub patches. Changes in the abundance of perennial grass species among sites may be primarily attributed to a high direct effect of grazing on the species with the most mesophytic and acquisitive traits (N-rich green tissues, high leaf production, and low lignin concentration in leaves). Under grazing exclusion, this species was the most associated with shrub patches. The other perennial grass species either did not reduce or increased their abundance with grazing. The species with a mix of mesophytic and xerophytic traits was found with high frequency at inter-patch microsites. The most xerophytic and conservative species occupied vacant microsites either between shrub patches or at shrub-patch centres. However, the three species were increasingly concentrated under shrub canopies with increasing grazing pressure. This fact stresses the importance of shrub patches as biotic refuges for perennial grasses with low anti-herbivore defences.

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1. Introduction

Plant cover usually displays some degree of spatial heterogeneity that can be identified at different scales (Dale, 1999) influencing biogeochemical fluxes, biotic/abiotic interactions, and plant responses to disturbance at different organisation levels (de Blois et al., 2002). In arid ecosystems, the vegetation is patchily distributed forming a two-phase mosaic composed by discrete units of high plant cover (shrub patches) distributed on a matrix of bare soil and/or scattered herbaceous plants (Aguiar and Sala, 1999). Shrub patches concentrate nutrients, water, organic matter, litter, seeds, and microbiological activity and modify the abiotic environment (Bertiller, 1998; Schlesinger and Pilmanis, 1998). This in turn promotes the emergence, establishment, and growth of perennial grasses and other herbaceous plants in the neighbourhood of shrub patches (Aguiar and Sala, 1999; Bisigato and Bertiller, 2004). Additionally, due to the presence of physical and chemical defences against herbivores, shrubs have poor food quality, are occasionally grazed (Baldi et al., 2004; Lauenroth, 1998), and protect preferred perennial grasses from grazers under their canopies (Milchunas and Noy-Meir, 2002).

Grazing by domestic herbivores affects the spatial structure and floristic composition of arid plant communities inducing fine-scale spatial modifications in the availability of soil resources (Rietkerk et al., 2000; van de Koppel et al., 2002). These changes affect the quantity and quality of microsites available for the emergence and recruitment of perennial grass populations (Bisigato and Bertiller, 2004; Cheplick, 1998; Oesterheld and Sala, 1990). This plant life form is one of the most preferred by large herbivores and sensitive to continuous grazing disturbance (O'connor, 1991). The removal of green tissues by grazers may lead to reduced bunch vitality, increased bunch death, and reduced sexual recruitment by reduced seed rain (Augustine and McNaughton, 1998; Ferraro and Oesterheld, 2002; O'connor and Everson, 1998).

Many studies described responses to grazing of herbaceous plants in terms of species abundance at different arid and semiarid ecosystems (e.g. Adler et al., 2005; McIntyre and Lavorel, 2001; Vesk and Westoby, 2001). Other studies analysed the effect of grazing on the spatial distribution of perennial grass species in relation to the shrubby matrix and found that perennial grasses could display random, associated, or dissociated spatial distributions with respect to shrubby canopies (Abule et al., 2005; Cipriotti and Aguiar, 2005; Landsberg et al., 1999). However, the causes of differences in the spatial patterning among species of this life form with low anti-herbivore defences have been scarcely studied. These differences among perennial grass species could be associated with differences in their functional traits (Augustine and McNaughton, 1998; Craine, 2005; Hutchings et al., 2003). In this sense, species with high relative growth rate, low leaf mass per area, high nitrogen concentration, and low physical/chemical defences in green tissues (Díaz et al., 2004; Hartley and Jones, 1998; Westoby et al., 2002) could be benefited from the high resource availability and anti-herbivore protection under shrub canopies (Hutchings et al., 2003; Milchunas and Noy-Meir, 2002). In contrast, slow-growing perennial grasses with high investment in structural tissues could better tolerate both abiotic stress and herbivory at less protected resource-poor inter-patch spaces (Augustine and McNaughton, 1998; Grace, 1998; Hutchings et al., 2003). To test these hypotheses, we selected three dominant perennial grasses with contrasting functional traits and assessed their abundance (density, bunch size) and spatial patterning in relation to the shrubby matrix at sites with different grazing pressure in the arid Patagonian Monte.

2. Methods

2.1. Study area

This study was carried out in the Patagonian Monte, at the northeastern portion of Chubut province, Argentina (42–44°S and 64–68°W) (León et al., 1998). Mean annual precipitation is 235.9 mm with high mean inter-annual variation (www.centropatagonico.com). Although the inter-seasonal variation of precipitation is low, a relative maximum occurs in autumn–winter. Soils are a complex of typical petrocalcids–typical haplocalcids (Soil Survey Staff, 1998).

The study sites were located within a representative area of the dominant community of *Larrea divaricata* Cav. and *Stipa* spp. (León et al., 1998). Vegetation covers from 40% to 60% of the soil and it is patchily arranged (Bisigato and Bertiller, 1997). Large shrub-grass patches are characterised by an upper layer (1–2 m) dominated by tall shrubs (*L. divaricata*, *Schinus johnstonii* Barkley, *Chuquiraga hystrix* Don., *Atriplex lampa* Gill. ex Moq., and *Lycium chilense* Miers ex Bert.), an intermediate layer (0.3–1 m) composed by dwarf shrubs (*Nassauvia fuegiana* (Speg.) Cabrera, *Junellia seriphioides* (Gillies and Hook) Mold., and *Acantholippia seriphioides* (A. Gray) Mold.), and a low layer (0.1–0.4 m) dominated by perennial grasses (*Stipa tenuis* Phil., *S. speciosa* Trin. and Rupr., and *Poa ligularis* Nees ex Steud) (Bisigato and Bertiller, 1997). Nomenclature follows Correa (1971–1999). In this region, sheep grazing was introduced at the beginning of the past century and is usually organised in ranches of about four large paddocks of ca. 2500 ha each sharing a single permanent watering point (Ares et al., 2003).

2.2. Perennial grass species and functional traits

We selected the three dominant perennial grass species in the Patagonian Monte: *P. ligularis*, *S. tenuis* and *S. speciosa*, which constitute more than 90% of herbaceous biomass of the plant community. Other perennial grass species appear at very low frequency and biomass at both grazed and non-grazed areas. We characterised each perennial grass species through 10 functional traits related to resource acquisition/conservation, mesophytism/xerophytism, apparency (*sensu* Feeny, 1976), and reproductive strategy. Accordingly, high values of lignin concentration in leaves, seed length, LMA, leaf pubescence, and plant height were interpreted as characteristic of conservative/xerophytic plants while high values of leaf turnover, leaf production, leaf length, and nitrogen concentration in leaves were interpreted as acquisitive/mesophytic traits (Adler et al., 2004; Díaz et al., 2004; Hartley and Jones, 1998; Westoby et al., 2002). Dioecy in *P. ligularis* could be interpreted as an intermediate acquisitive/conservative strategy since the sexes of this species show spatial segregation with males occupying more xerophytic microsites than females (Bertiller et al., 2002b). The values of eight of these traits were taken from previous studies: nitrogen concentration in green leaves, leaf mass per area (Bertiller et al., 2005), rate of leaf turnover (Carrera et al., 2000), leaf length, leaf pubescence, plant height, seed length, and reproductive strategy (monoecy/dioecy) (Correa, 1978). Lignin concentration in green leaves and the rate of leaf production were assessed in this study. We measured lignin concentration in green leaves of bunches of the three perennial grass species collected in May–June of 2000 and 2001 by the van Soest (1963) procedure. We assessed the rate of leaf production as the mean number of new leaves emerged per tiller and per week in 10 randomly selected individuals of

each species (one tiller per individual) at 15-day intervals in a non-grazed area located in Estancia San Luis during the growing season from August (mid-winter) 2003 to January (mid-summer) 2004. We performed a principal components analysis (PCA) to identify associated traits using the matrix of binary correlations between traits. For ordination of perennial grass species according to these traits, we further calculated the loading coefficients of each species with respect to the first two principal components (Noruși, 1997).

2.3. *Field sampling*

We selected five paddocks of 2500 ha each with the usual stocking rate for the area (0.17–0.22 sheep per ha). Three of them were located at Estancia San Luis (42°39'S, 65°23'W) and the other two paddocks were located at Estancia El Milagro (42°43'S, 65°38'W). Within each paddock, we selected two sites of about 2 ha each at 0.5–1 km and at 4–5 km from the permanent watering point. Based on previous analysis on floristic composition, faeces counts, and plant patterning (Bisigato and Bertiller, 1997; Bertiller et al., 2002a), we assumed that these locations correspond to sites with high (H) and low (L) past and present grazing pressure, respectively. To test this assumption, we assessed the density of sheep paths at four transects (50 m in length) placed along the arc of an imaginary circle around the watering point at both sites within each paddock (Pringle and Landsberg, 2004). We registered the number of well-defined sheep paths crossing each transect, taking special attention in avoiding small runoff paths. Minor local anastomoses were considered as single tracks. The significance of the differences in the density of sheep paths per km between L and H sites was assessed by paired-samples *T*-test (Noruși, 1997).

We further selected two sites of about 2 ha each excluded from grazing for at least the last 15 years (EX) within paddocks of ca. 2500 ha. The paddocks were separated 10 km one from the other and were situated at Estancia Gallastegui (42°44'S, 65°07'W) and at Laguna Blanca (42°48'S, 65°08'W).

At each site (EX, L, and H at each paddock), we delimited four 50 m linear transects (two SW to NE and two NW to SE oriented) and recorded the position and intercepted diameter of shrub patches and bunches of the three dominant perennial grass species along each transect. We defined a grass bunch as a group of tillers isolated from other group of the same species by a minimum distance of 5 cm and a shrub patch as a discrete cluster of shrub canopies separated from other cluster by at least 5 cm of bare soil.

2.4. *Abundance of perennial grasses and shrub patches*

At each site, we calculated the mean density (number of bunches per 50 m-transect) and mean intercepted diameter of each perennial grass species, and the mean cover, density (number of shrub patches per 50 m-transect), and intercepted diameter of shrub patches. The significance of the differences in these variables among sites (EX, L, and H) was assessed by means of one-way ANOVA after testing for statistical assumptions (Noruși, 1997).

2.5. *Spatial patterns of perennial grasses*

The spatial pattern of perennial grasses in relation to shrub patches was assessed by analysing the relative frequency distribution of distances between the centre of each perennial grass bunch and the nearest shrub patch border along each transect. We assigned

negative distance values to bunches located inside shrub patches and positive values to those located at the open inter-patch spaces. Zero distances corresponded to bunch centres at the shrub patch border. We pooled the measured distances at the four transects within each site and paddock and calculated the relative frequency distribution of distances using distance classes of 25 cm ($n = 10$). Then, we estimated the overall relative frequency distribution of distances of each perennial grass species for EX, L, and H sites as the mean of the relative frequency of each distance class across paddocks. It should be noted that distances of grass bunches to shrub patch borders could be larger or lower than mean intercepted diameters of shrub patches at each site.

We compared the observed relative frequency distributions with those expected by assuming a null bivariate spatial process (independence between the spatial patterns of shrubs and perennial grasses) following the approach proposed by Wiegand and Moloney (2004). Confidence intervals of the null model for each site and paddock were built by randomising (1000 times) the position of the grass bunches (all species pooled) in relation to shrub patches along each transect. After that, we generated 1000 random frequency distributions of the distances of perennial grasses to shrub patch borders for EX, L, and H sites by averaging the relative frequency of each distance class obtained from each randomisation across paddocks. Randomisations were achieved using the PopTools package (www.cse.csiro.au/CDG/poptools). We used the Bonferroni correction (alpha/number of distance classes) for estimating the confidence intervals in order to obtain a global error of 5% for each species at each site. We considered deviations from the null model when the observed frequency at each distance class was higher or lower than the maximum or the minimum limit of the confidence interval, respectively (Manly, 1997). Moreover, we assigned the values -1 , 0 , or 1 to each distance class when the observed frequencies were lower, equal, or higher, respectively, than those expected by the null model. Thus, we obtained one vector ($n = 10$) per species and site (EX, L, and H) of deviations from the null model. We performed PCA using the matrix of binary correlations between vectors (Norusis, 1997) for clustering species per site with similar deviations from the null model.

3. Results

3.1. Functional traits of perennial grasses

Most acquisitive/mesophytic traits were clustered at negative values of PCA axis 1 (71% of the total variance) while conservative/xerophytic traits were grouped at positive values of PCA axis 1. On this PCA axis, *S. speciosa* was clustered with high values of lignin concentration in leaves, leaf mass per area, seed length, and plant height. In contrast, *S. tenuis* and *P. ligularis* had almost the same negative value on PCA axis 1 but differed on PCA axis 2 (29% of the residual variance). High N concentration in leaves, leaf pubescence, and high leaf production were clustered with *S. tenuis* at positive values of PCA axis 2. At negative values of this PCA axis, *P. ligularis* was clustered with high leaf turnover, high N concentration in green leaves, and dioecy (Fig. 1; Table 1).

3.2. Sheep paths, and attributes of the shrubby matrix

The number of sheep paths per km was significantly higher at sites located at 0.5–1 km (H) than those at 4–5 km (L) from the permanent watering point ($t = -6.56$; $df = 4$;

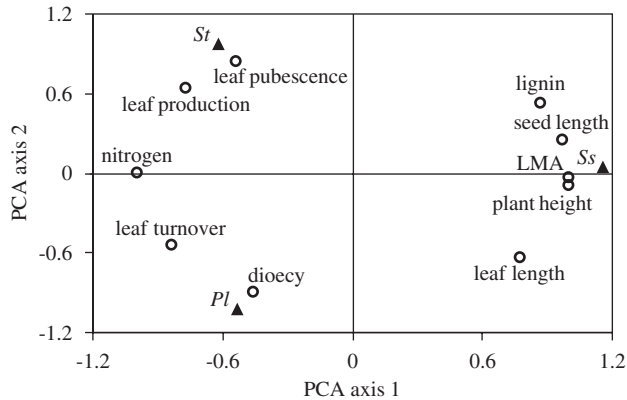


Fig. 1. Ordination of plant functional traits (circles) as in Table 1, and species (triangles) according to the first two PCA axes (PCA axis 1: 71% and PCA axis 2: 29% of the total variance). LMA: leaf mass per area (g m^{-2}). *Pl*: *Poa ligularis*, *St*: *Stipa tenuis*, and *Ss*: *S. speciosa*.

Table 1
Plant functional traits of the three perennial grass species

Trait	<i>Poa ligularis</i>	<i>Stipa tenuis</i>	<i>Stipa speciosa</i>
Nitrogen concentration in green leaves (%) ^a	2.79	2.85	1.63
Lignin concentration in green leaves (%) ^b	3.03 ± 0.32	4.47 ± 0.51	6.18 ± 0.45
Leaf mass per area ($\text{g dry weight m}^{-2}$) ^a	153	144	258
Leaf turnover rate (ranking among other species) ^c	6	5	4
Leaf production rate (leaves week ⁻¹) ^b	0.118 ± 0.016	0.212 ± 0.042	0.085 ± 0.011
Leaf length (cm) ^d	10–20	5–10	12–25
Leaf pubescence ^d	–	+	–
Plant height (cm) ^d	15–45	15–40	30–60
Seed length (mm) ^d	1.5–2.8	5.0–8.0	10.0–12.0
Reproductive strategy ^d	Dioecy	Monoecy	Monoecy

For lignin concentration in green leaves and leaf production rate, mean values \pm 1 SE are given. For leaf pubescence, (+) and (–) indicate presence and absence of the trait, respectively.

^aBertiller et al. (2005).

^bThis study.

^cCarrera et al. (2000).

^dCorrea (1978).

$p < 0.01$) (Table 2), indicating higher intensity of use by sheep at H than at L sites. The cover of shrub patches did not vary among sites, but their density was lower at sites excluded from grazing (EX) than at both grazed sites (L and H). The highest intercepted diameter of shrub patches occurred in EX and the lowest in L sites. The density and intercepted diameter did not significantly differ between L and H sites (Table 2).

3.3. Density, size, and spatial patterning of perennial grasses

The density of *P. ligularis* decreased from EX to H sites, whereas the largest density of *S. speciosa* occurred at L sites. In contrast, the density of *S. tenuis* did not vary among sites

Table 2

Mean values \pm 1SE of density of sheep paths, and cover, density, and intercepted diameter of shrub patches at sites excluded from grazing (EX) and with low (L) and high (H) grazing pressure

	Sites		
	EX	L	H
Density of sheep paths (sheep paths per km)	—	47 \pm 8.9 ^a	162 \pm 18.3 ^b
Shrub cover (%)	36.3 \pm 1.3 ^a	37.1 \pm 1.3 ^a	40.5 \pm 3.9 ^a
Shrub density (number of shrub patches per 50 m transect)	15.9 \pm 1.6 ^a	24.0 \pm 1.5 ^b	23.5 \pm 0.7 ^b
Intercepted diameter (cm)	115.1 \pm 7.8 ^b	78.2 \pm 4.7 ^a	86.2 \pm 7.9 ^{ab}

Different lower case letters indicate significant ($p < 0.05$) differences among sites.

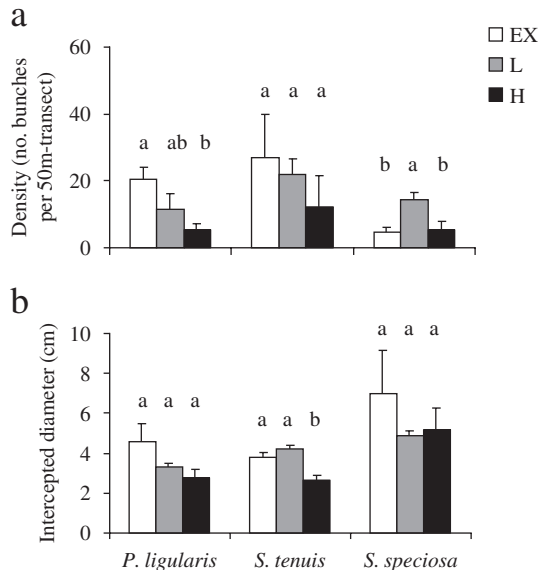


Fig. 2. Mean values of bunch density (a), and intercepted diameter (b) of perennial grasses at sites excluded from grazing (EX) and with low (L) and high (H) grazing pressure. Vertical lines indicate 1SE. Different lower case letters indicate significant differences ($p < 0.05$) among sites for each species.

(Fig. 2a). The mean intercepted diameter of *P. ligularis* and *S. speciosa* did not vary among sites while that of *S. tenuis* was reduced at H sites (Fig. 2b).

At sites excluded from grazing, *P. ligularis* showed higher frequency of bunches at distances near patch borders (from 0 to -25 cm), and lower frequency near patch centres (-75 to -100 cm) and far away outside shrub patches (> 100 cm from patch borders) than expected by chance. At L sites, this species showed higher frequency of bunches than expected inside shrub crowns (0 to -75 cm) and lower frequency at almost all distance classes outside them. At H sites, the frequency of *P. ligularis* was higher and lower than expected at most distances inside and outside shrub crowns, respectively (Fig. 3a).

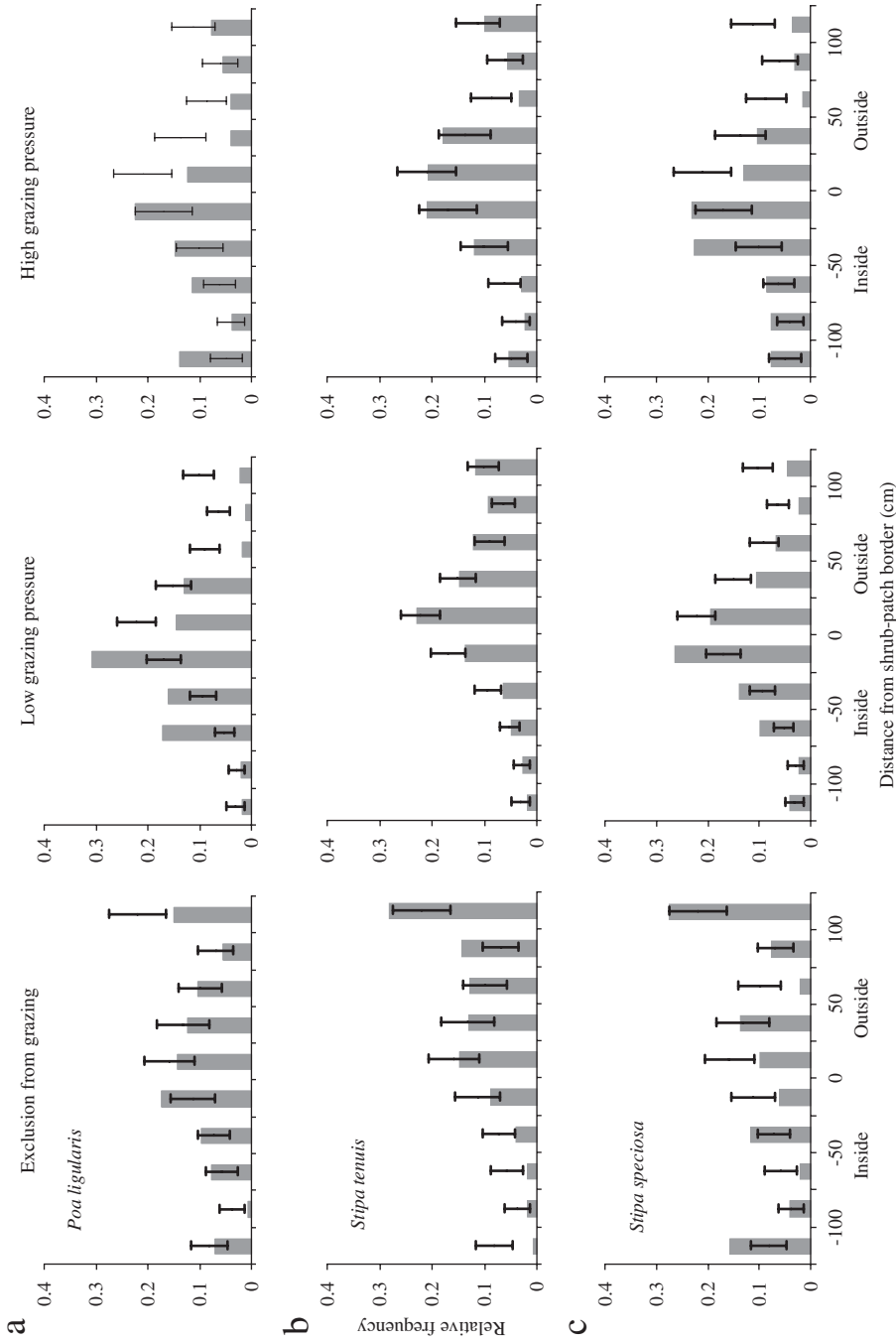


Fig. 3. Observed relative frequency (bars) of perennial grasses at different distance intervals to the border of the nearest shrub patch at sites with different grazing pressure. Zero, negative, and positive values indicate perennial grasses at the border, inside, and outside of shrub patch canopies, respectively. Vertical lines represent the Bonferroni-corrected confidence interval ($\alpha = 0.05$, 10 distance classes) of the null model of spatial independence between shrub patches and perennial grasses. Observed frequencies larger than the maximum limit or smaller than the minimum limit of each confidence interval indicate significant deviations from the null model. A site-by-site analysis is provided in the Appendix A.

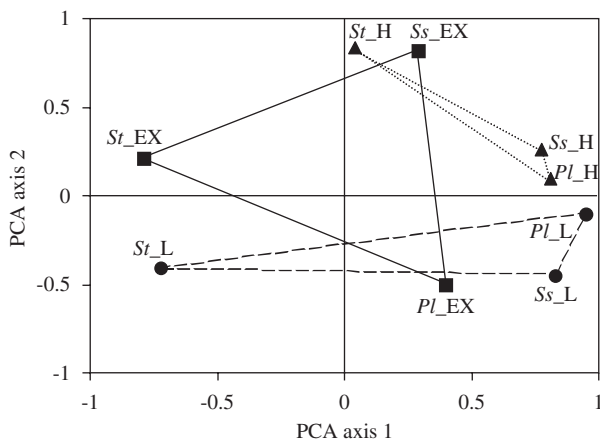


Fig. 4. Ordination of vectors of spatial patterning of the three species at each site: EX (squares, solid line), L (circles, dashed line), and H (triangles, dotted line) according to the first two PCA axes (PCA axis 1 and 2: 47% and 23% of the total variance, respectively). Acronyms for species and sites as in Figs. 1 and 2, respectively.

S. tenuis showed higher frequency than expected at distances >75 cm from the patch borders and lower frequency at most distances inside shrub canopies at EX sites. At L sites, this species showed higher frequency of bunches between 50 and 100 cm outside shrub canopies and lower frequencies than expected inside shrub canopies (0 to –50 cm). At H sites, the frequency of *S. tenuis* was lower than expected at distances from –50 to –75 cm (inside) and 50 to 75 cm (outside shrub canopies) (Fig. 3b).

At EX sites, *S. speciosa* showed lower frequency than expected at distances near to shrub patch borders (–25 to 25 cm) and at mid distances inside (–50 to –75 cm) and outside (50 to 75 cm) patch crowns. This species also showed higher frequency than expected inside patches (–25 to –50 cm and <–100 cm) and at distances far away outside shrubs (>100 cm). At L sites, the frequency of bunches was higher than expected at 0 to –75 cm inside, and lower than expected at most distances outside shrub canopies. At H sites, this species showed higher frequency of bunches than expected at 0 to –50 and –75 to –100 cm inside shrub patches, and lower than expected at most distances outside shrub patches (Fig. 3c).

The ordination of the spatial patterns of the three species according to the first two PCA axes (PCA axis 1 and 2: 47% and 23% of the total variance, respectively) indicated that the three species showed contrasting spatial distributions at EX sites. *S. tenuis* was located at negative values of PCA 1 and positive values of PCA 2, *S. speciosa* at positive values of both PCA axes, and *P. ligularis* at positive and negative values of PCA axis 1 and 2, respectively. At L sites, the spatial patterning of *S. tenuis* (negative values of PCA 1) differed from those of the other species across PCA 1 (positive values of PCA 1) and converged across PCA axis 2 (negative values). At H sites, the spatial patterning of all species converged at positive values of both PCA axes (Figs. 3 and 4).

4. Discussion

P. ligularis and *S. tenuis* showed acquisitive/mesophytic traits related to high relative growth rate and potential for resource capture while *S. speciosa* displayed conservative/

xerophytic traits associated with low relative growth rate, high potential for resource conservation, and high investment in structural compounds (Díaz et al., 2004; Hartley and Jones, 1998; Westoby et al., 2002). We found evidence for the effect of grazing on the abundance of perennial grass species with different functional traits but the spatial patterning of these species with respect to the shrubby matrix was not differentially affected by grazing. Further, the cover of the shrubby matrix was not affected by grazing although increased density and reduced diameter of shrub patches were observed in sites disturbed by grazing as reported elsewhere (Adler et al., 2001; Bisigato and Bertiller, 1997; Bertiller et al., 2002a; Cipriotti and Aguiar, 2005).

In terms of abundance, the decrease in density of *P. ligularis* with increasing grazing pressure without changes in bunch size is consistent with high direct grazing impact on this species through a high rate of removal of high-quality green tissues (high N concentration, low leaf mass per area, and low lignin concentration) and subsequent bunch death (Adler et al., 2004; Augustine and McNaughton, 1998; Ferraro and Oesterheld, 2002). In addition, reduced abundance of *P. ligularis* in grazed areas could be associated with an indirect effect of grazing through changes in the shrubby matrix. Small shrub patches in grazed sites could affect sexual recruitment through harsher local microenvironmental conditions in their neighbourhood relative to large patches (Bertiller, 1998; Bertiller et al., 2002b; Maestre and Cortina, 2005; Mazzarino et al., 1996). In contrast, the abundance of *S. tenuis* did not vary among sites with different grazing pressure probably due to lower herbivore preference for this species with more xerophytic traits (pubescent leaves and low leaf length) than *P. ligularis*, and also low apparency. These results are consistent with lower herbivore preference for *S. tenuis* relative to *P. ligularis* reported by Elissalde and Miravalles (1983) and reduced herbivore preference for plant tissues with xerophytic traits described in other studies (Coughenour, 1985; Hartley and Jones, 1998). However, bunch size (diameter) of this species was reduced at high grazing pressure, a fact that could be traced back either to a direct effect of grazing on this species through tissue removal (Ferraro and Oesterheld, 2002) or to high sexual recruitment in this species producing small and abundant seeds (Bisigato and Bertiller, 1997; Mayor et al., 2003). Contrarily to the other two species, *S. speciosa* showed enhanced bunch abundance under low grazing pressure. This is consistent with the lowest herbivore preference for this species as compared to the other two perennial grasses (Elissalde and Miravalles, 1983), probably due to strong xerophytic/conservative traits such as high lignin and low N concentration in green leaves, and high leaf mass per area (Adler et al., 2004). However, preference by herbivores cannot explain lower abundance of this species at sites excluded from grazing relative to sites with low grazing pressure. Probably, *P. ligularis* and *S. tenuis* with more mesophytic/acquisitive traits than *S. speciosa* would outcompete this latter at sites protected from grazing (Bertiller et al., 2002b; Lauenroth and Aguilera, 1998).

The spatial patterning of the three perennial grass species relative to the shrubby matrix was not differentially affected by grazing. In sites excluded from grazing the three species displayed contrasting spatial patterns consistent with their functional traits. *P. ligularis*, having the strongest mesophytic and acquisitive traits, occupied at high density sheltered N-rich microsites at shrub patch borders. *S. tenuis* with both mesophytic and xerophytic traits and the highest bunch density was more abundant than expected in open resource-poor inter-patch spaces (Bertiller et al., 2002b; Mazzarino et al., 1996). Furthermore, *S. speciosa*, with the strongest xerophytic and conservative traits occupied, at very low density, vacant microsites of highly contrasting quality either near patch centres or outside

patch crowns. Probably, the high bunch density of both *P. ligularis* and *S. tenuis* and their spatial patterning reflect higher competitive ability and enhanced sexual recruitment relative to *S. speciosa* in sites excluded from grazing with the largest shrub patches (Fernández et al., 2002; Ghermandi, 1997).

Despite the contrasting spatial patterning of the three species at sites excluded from grazing, increasing grazing pressure led to the concentration of bunches underneath shrub canopies. This stressed the importance of shrub patches as biotic refuges for perennial grasses in shrublands disturbed by grazing (Callaway et al., 2005; Milchunas and Noy-Meir, 2002). However, *S. tenuis* maintained high abundance and the widest spatial distribution in relation to patch canopies under high grazing pressure, probably due to its low apparency, the presence of xerophytic traits, and high sexual recruitment (Bisigato and Bertiller, 1997; Mayor et al., 2003).

We concluded that our results do not support the hypothesis that grazing affects differently the spatial patterning of perennial grass species with different functional traits. The greatest contrast in the spatial patterning among species with different functional traits was found at sites excluded from grazing, but increasing grazing pressure attenuated the differences leading to the confinement of bunches underneath well anti-herbivore defended shrub-patch canopies. The wide spatial distribution and the high abundance of *S. tenuis* in grazed areas suggest that the combination of functional traits related to fast growth and stress tolerance constitutes an adaptive advantage in water-limited environments.

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Appendix A. Supplementary materials

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.jaridenv.2006.12.025.

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