

Effect of grazing on plant patterns in arid ecosystems of Patagonian Monte

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Our objective was to assess the relationship between the spatial patterning of perennial grasses (total, grazed, and non-grazed) and shrub patches in rangelands under different grazing pressures of the Patagonian Monte. We selected three grazed paddocks with the usual stocking rate for the area, where previous studies showed that a piosphere formation is common. At each paddock, we analysed the grain of heterogeneity at sites located at two distances from the single watering point (near, far), using high-resolution aerial photographs. At these sites, we also assessed in the field the density, size, cover, and spatial patterning of grazed and non-grazed perennial grasses and shrub patches. The grain of heterogeneity of shrub patches was coarser in sites near the watering point than in those distant from it, as a consequence of the increase in size of both, bare soil and shrub patches. Field sampling showed that a coarse grain of heterogeneity relative to fine-grained sites resulted from changes in species composition, increased bare soil areas and reduced perennial grass cover. In coarse-grained sites, lower perennial grass cover resulted from lower density and/or smaller size of grass bunches than in fine-grained sites. We did not find significant differences among sites in the proportion of perennial grazed grasses. Since the density and cover of perennial grasses was higher in fine- than in coarse-grained sites, we suggested that fine-grained sites are more important as feeding stations than coarse-grained sites. The consequences of this differential use could lead to degradation of fine-grained sites and to higher homogeneity in spatial plant structure and floristic composition within paddocks with respect to the condition observed at present, increasing the size of the highly degraded zone within the piosphere. At the patch level, we found that at about one third of the sampled transects, both total and non-grazed perennial grasses were spatially aggregated with shrub patches. However, in most transects grazed perennial grasses were indifferently distributed in relation with shrub patches, showing that grazers display high selectivity of foraging sites at macro level (i.e. high and low grazing pressure sites at the paddock level), but random occupancy of vegetation units (randomness in the distribution of grazed perennial grasses at the patch level). The intensity of the positive association between non-grazed grasses and shrub patches was higher in fine-grained than in coarse-grained sites and may be attributed to higher protection against herbivores associated to denser shrub patches in fine- relative to coarse-grained sites. We concluded that a feedback exists between the spatial distribution of species preferred by grazers and the spatial patterning of use of these species.

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The study of plant spatial patterns and their consequences for ecological processes has received increasing attention during the last twenty-five years (Liebhold and

Gurevitch 2002) due to a change in the dominant prevailing ecological paradigms. The prevailing concept of homogeneity and equilibrium associated with natural

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ecosystems was gradually changed by the heterogeneity and non-equilibrium paradigm (Sparrow 1999). Consequently, new questions arose in relation to spatial heterogeneity, its determinants and its consequences for ecological processes (Schwinning and Parsons 1999, Adler et al. 2001).

Plant spatial heterogeneity is one of the most conspicuous features of desert ecosystems (Aguilar and Sala 1999, Tongway et al. 2001). Thus, arid plant communities could be viewed as a two-phased mosaic consisting of a high-covered phase and other phase of bare soil or scattered plant cover (Aguilar and Sala 1999). Woody plants (trees and/or shrubs) usually dominate phases of high plant cover, while herbaceous elements may be either scattered or associated with woody components (Scholes and Archer 1997). This spatial organisation of vegetation, either banded or spotted, has important consequences for the heterogeneity of soil resources and ecosystem functioning (Ludwig and Tongway 1995). In spotted vegetation, above- and belowground litter is decomposed and mineralised producing a regular gradient in nutrient availability from the soil surface downwards and from the centre of plant patches to the inter-patch areas (Facelli and Brock 2000). Plant patches may also accumulate resources mobilised either from inter-patch areas via wind or runoff and/or from deep soil layers through deep roots (Horton and Hart 1998). Another source of heterogeneity is the sheltering effect of patch canopies creating ameliorated microclimatic conditions inside and/or nearby patch canopies improving the suitability of these microsites for seedling establishment (Callaway 1995). Ameliorated microclimatic conditions are not only relevant during the early developmental stages of plant canopies, but they may also have beneficial effects for plant establishment in mature phases of patch development (Facelli and Brock 2000).

Several authors found that plant patches are main nuclei of herbaceous-plant establishment, at least during early stages of patch development (Belsky et al. 1989, Soriano et al. 1994, Bisigato and Bertiller 2004a). Conversely, other authors have reported a homogeneous distribution of herbaceous plants among different microsites with respect to established vegetation (Holm et al. 2002b) or higher frequency of herbaceous plants in bare soil areas relative to areas nearby shrub patches (Weltzin and Coughenour 1990). Additionally, the woody components of plant patches may protect herbaceous plants from herbivory when they have spines or another herbivore-deterrent structure (Milchunas and Noy-Meir 2002). Inversely, local high density of grasses may lead to high use of neighbouring shrubs (Palmer et al. 2003).

Desertification deeply affects the characteristics of soil (Schlesinger and Pilmain 1998), vegetation (Reynolds et al. 1997) and animal (Whitford 1997) components of

ecosystems. Grazing has been identified as one of the main factors leading to arid land desertification. Other causes such as climate and global change have also been proposed as relevant influences (Fernández 2002). Grazing frequently operates through the reduction of plant cover and fragmentation followed by disappearance of vegetation patches, reducing their size and/or numbers and leading to soil erosion and losses of nutrients from the exposed soil (Holm et al. 2002a). In addition, relict patches may capture many nutrients mobilised from exposed soil areas (Bhark and Small 2003) becoming nutrient-richer in comparison to those in conserved areas. Despite this, the overuse by grazing of these remnant resource-rich patches could result in irreversible vegetation changes (van de Koppel et al. 2002). These changes are generally characterized by the replacement of grasses by woody species, leading to shrub and/or tree invasion and the concomitant increase in the scale of spatial pattern of plant patches and soil resources (Schlesinger et al. 1996, Reynolds et al. 1997, Adler et al. 2001).

The analysis of the spatial patterning of palatable plants in grazed areas may be an adequate indicator of land degradation by grazing and a clue to interpret further consequences of grazing on plant and soil processes and on the grazers themselves (Dumont et al. 2002). It has been proposed that the behaviour of grazers is in essence a hierarchical process resulting from decisions taken at different spatio-temporal scales that are defined by the rates of foraging processes (Senft et al. 1987). Diet selection decisions take place more often at small scales (feeding stations or communities) than at large scales (regions or landscapes). The importance of small-scale decisions is particularly relevant in domestic grazing systems, where the movement of grazers is frequently reduced by property's boundaries (Bailey et al. 1996). The changes in the fine-scale spatial pattern of plant resources can strongly affect the behaviour of herbivores (Dumont et al. 2002, Oom et al. 2002). For example, fine-grained resources may reduce the ability of grazers to select more productive patches, resulting in a more homogeneous grazing pattern (Hester and Baillie 1998). Similarly, fine-grained resources could limit the group size of gregarious grazers, resulting in a more homogeneous grazing pattern as compared to coarse-grained resources (Clarke et al. 1995, Johnson et al. 2002). In addition, patches constituted by shrubs with spines and/or other structural defences against herbivores frequently may be less grazed than other patches or sparse vegetation without anti-herbivore defences, thus resulting in more heterogeneous grazing patterns (Milchunas and Noy-Meir 2002).

Although evidences of different grazing behaviour of herbivores as a consequence of changes in the spatial pattern of vegetation have been intensively explored in humid or sub-humid ecosystems (Clarke et al. 1995)

there are only few studies addressing feedbacks between spatial plant structure and grazing behaviour in degraded arid ecosystems. In this context, Patagonian Monte ecosystems are adequate in order to test hypotheses related to this subject. As other arid ecosystems of the world, vegetation in the ecosystems of the Patagonian Monte is characterised by shrublands, with variable grass cover, low total cover and patchy structure (Bisigato and Bertiller 1997). At a landscape scale (5–50 km), gradients of pattern change of plant patches related to the impact of grazing in the Patagonian Monte have been recently assessed by high-resolution aerial photographs (Ares et al. 2003a). Patches strongly influence the distribution of resources such as seeds (Bertiller 1998), nutrients (Carrera et al. 2003), water (Bisigato and Bertiller 2004b), and microclimatic conditions (Bertiller et al. 2002a). Preliminary studies showed that shrub patches are nuclei of grass establishment (Bisigato and Bertiller 1999, 2004a). Sheep grazing was introduced at the beginning of the last century, affecting species composition and the spatial pattern of plant patches (Ares et al. 2003a). As a consequence of the location of the watering points, different grazing pressures frequently occur within paddocks leading to the formation of a piosphere within them. Intensively grazed areas show changes in the structure of plant patches resulting from lower species richness, lower plant cover, lower grass cover, and larger relative shrub cover than lightly-grazed areas (Bisigato and Bertiller 1997, Bertiller et al. 2002b).

Our objective was to assess the relationship between the spatial patterning of perennial grasses (total, grazed, and non-grazed) and shrub patches in rangelands of the Patagonian Monte resulting from different distances to watering points under different grazing pressures. We hypothesised that 1) grazing pressure would modify the grain of spatial heterogeneity of shrub patches, and 2) the association between perennial grasses and shrub patches and the pattern of use of perennial grasses by sheep would vary in relation to the grain of spatial heterogeneity of shrub patches. Accordingly, we expected 1) coarser grain of spatial heterogeneity in sites near watering points relative to those far away from watering points and, 2) stronger association between perennial grasses and shrub patches, and between non-grazed grasses and shrub patches in coarse- than in fine-grained sites.

Methods and materials

Study area

The study area is representative of the Patagonian Monte (León et al. 1998) located in north-eastern Chubut Province, Argentina (42°39'S, 65°23'W, 115 m a.s.l.). Annual-mean temperature is 13.4°C and average

precipitation is 235.9 mm with high mean inter-annual variation (Anon. 2005). Soils are a complex of Typic Petrocalcids – Typic Haplocalcids (Anon. 1998). Dominant vegetation is the community of *Larrea divaricata* and *Stipa* spp. (Bisigato and Bertiller 1997). In this community, *L. divaricata*, *Chuquiraga hystrix*, *Lycium chilense*, *Schinus johnstonii*, and *Atriplex lampa* dominate the upper vegetation layer (1–2 m), while the lower layer (<1 m) is composed by perennial grasses (*Stipa tenuis*, *S. speciosa*, *S. humilis* and *Poa ligularis*) and dwarf shrubs (*Nassauvia fuegiana*, *Acantholippia seriphoides*, and *Junellia seriphoides*) (Bisigato and Bertiller 1997). Spines and other structural defences against herbivores are very frequent among shrubs (Lauenroth 1998). In consequence, shrubs are not a major component of sheep diet at any time of the year (Baldi et al. 2004). Field observations were conducted in three paddocks (ca 2500 ha each), sharing a single permanent watering point, with the usual stocking rate for the area (0.11–0.14 sheep ha⁻¹).

Selection of field sampling sites

We used two sets of high-resolution aerial colour photographs of each of three paddocks taken in July 2002 at two ranges of distances from the watering point (near = 630–1200 m; far = 3400–4200 m), where we expected different spatial patterning of shrub patches due to the formation of piospheres around the permanent watering points (Ares et al. 2003a). At each photograph, we scanned three “windows” at 600 dpi using a palette of 256 grey tones, resulting in 6 windows per paddock (3 windows/photography × 2 photographs/paddock). The windows corresponded to areas of ca 100 × 100 m, with an approximate pixel resolution of 0.07 m. In the scanned windows dark pixels corresponded to shrub patches, while light pixels were associated with sparse small shrub patches and herbaceous vegetation or bare soil (Ares et al. 2003a). The digitised image files were then transported to a GIS application, where 20 linear profiles of image pixel values of length 858 pixels (ca 60 m) were extracted. The 3TLQV (3-term local quadrat variance) function of every profile was calculated. The algorithm examines the averages of squared values differences among sets (“blocks”) of three equal sized adjacent pixel groups. Each difference was calculated as twice the average value of the central group of pixels minus the corresponding to both side neighbours, and the process was repeated for the full range of possible block sizes and block starting positions along the profile. The procedure generated a variance-block size function, where the lowest block size at which a function local maximum occurs was interpreted as the “grain” size. In this procedure, the grain size is equivalent to the average distance between shrub

patch and contiguous inter-patch areas centres; grain size defined in this way depends on patch density and is independent of patch size (Dale 1999).

The relative importance of both phases (shrub patches/bare soil) in the pattern was inspected by NLV (new local variance). As in the case of 3TLQV, this method generates a variance-block size function, where the lowest block size at which a local maximum occurs corresponds to the average size of the smallest phase of the pattern (Dale 1999). In our study, this latter corresponds to shrub patches since shrubs never covered more than 27% of the soil surface (see Results). We calculated the proportion of shrub patches (PSP) in the pattern as:

$$\text{PSP} = \frac{0.5B_{\text{NLV}}}{B_{\text{3TLQV}}}$$

where: B indicates the block size at which a local maximum occurs in the new local variance (NLV) or three-term local quadrat variance (3TLQV) functions.

The significance of the differences in the non normally distributed grain sizes among photograph windows at the same distance and between distances from watering points was estimated through the randomisation test (Manly 1997). In each comparison, 1000 randomisations were achieved using the PopTools package <www.cse.csiro.au/CDG/poptools>. The significance of the differences in PSP among paddocks and distance from the watering point were inspected by two-way ANOVA of arcsine transformed data. We selected at each paddock two windows with significant ($p < 0.05$) different grain of heterogeneity as sites for field sampling.

Field sampling

Each selected site was delimited in the field and their floristic composition and plant cover was estimated (Mueller-Dombois and Ellenberg 1974, Bisigato and Bertiller 1997). Floristic similarity among sites was analysed using Euclidean distance and average linkage (Jongman et al. 1987).

In July 2003, we located four 50 m transects at each site in the field oriented from the site corners to their centre, to minimise eventual biases due to patch anisotropy (Ares et al. 2003b). Precipitation during the year 2003 was 219.9 mm. This value did not depart from the long-term average (235.9 mm) for the area (Anon. 2005). Along each transect, we recorded the presence of bunches of perennial grasses and shrub patches in 200 consecutive 25 cm segments. Each grass bunch was assigned to one of the following two groups: recently grazed bunches (those with at least one green leaf partially removed by grazing) and non-grazed bunches (those without grazed green leaves). Additionally, the percentage of grazed green leaves of each bunch was

visually estimated using categories with increments of 25%. Also, we measured the length of the segment intercepted by each bunch on the transect. The total perennial grass cover (%) and total grazed perennial grass cover (%) were calculated by the sum of all segments intercepted along the transect and the same weighed by the percentage of grazed green leaves, respectively, divided by transect length and multiplied by 100. The mean intercepted diameter (MID) of perennial grasses was also calculated averaging the length of all intercepted segments along each transect. The mean density of perennial grasses (grass bunches m^{-1} transect) was also computed by averaging the number of bunches intercepted per meter of transect. The significance of differences in mean density of grasses, mean grass cover, mean grazed perennial grass cover, proportion of grazed grasses, and MID between sites was inspected by a randomisation test (Manly 1997), when data failed to meet the assumption of homocedasticity.

Analysis of spatial association between grasses and shrub

We used covariance analyses to inspect the spatial arrangement of grasses with respect to shrubs. We analysed covariance with 3TLQC (3-term local quadrat covariance) to inspect the presence/absence (1, 0 respectively) of perennial grasses (grazed, non-grazed, and total) and shrub patches along each of the 24 field transects. The procedure was similar to the previously described 3TLQV, and covariances were calculated between two block-sampled data vectors (Dale 1999). Block sizes ranged from 0.25 to 7.5 m, an interval containing the grain size variation observed in the digitised site images (see Results). For each block size and transect, we constructed a null covariance model and associated 95% confidence intervals of 3TLQC values by calculating the covariance between each grass vector and the 23 shrub vectors assessed for the other transects. Since grass and shrub vectors of different transects can be considered independent, only 3TLQC values resulting from a grass vector and the corresponding shrub vector falling outside the null model range were considered as significant. Values greater than the upper confidence limit were interpreted as indicative of positive associations (aggregation) between perennial grasses and shrub patches, while those below the lower confidence limit were interpreted as indicating negative associations (segregation). Additionally, for each block size, we calculated the intensity of the association between perennial grasses and shrub patches (Dale 1999) as:

$$I_c(B) = \sqrt{6B|C(B)|/(B^2 + 2)}$$

where B is the block size and C the covariance estimated by 3TLQC. In this procedure, the intensity of covariance is proportional to the degree of pattern matching and to the relative importance of both phases in each pattern (Dale and Blundon 1991). Then, for each block size, we calculated the mean intensity of the pattern of covariance in fine- and coarse-grained sites averaging the values of the 12 transects of each grain (4 transects per site, 3 sites per grain).

Results

Selection of sites

The average grain (scale of patchiness) did not differ significantly ($p > 0.05$) among paddocks at a similar distance from the watering point but it differed significantly ($p < 0.05$) at different distances in the same paddock (Fig. 1). Areas located near watering points, where the grazing disturbance is high, showed greater grain size than those areas located far away from watering points. This increase in grain size was due to the enlargement of both phases (shrub patches and bare soil) since the relative contribution of shrub patches did not significantly vary with grain size. A set of 3 sites within “coarse” grain sized (3.72–4.19 m) photographs and another similar with “fine” grained (2.64–2.98 m) images were selected for detailed field study (see Fig. 2).

Site description

Coarse-grained sites showed lower total plant cover than fine-grained sites (Table 1). Species composition

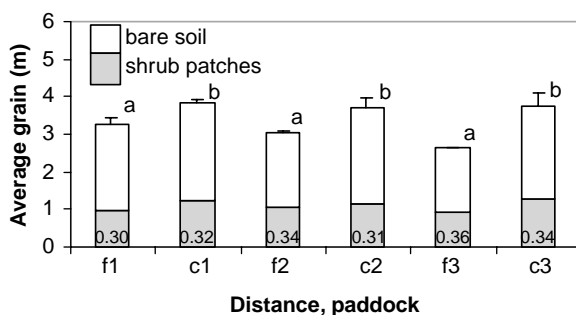


Fig. 1. Average grain (scale of patchiness) and contribution of each phase to the pattern at all scanned windows of aerial photographs inspected for site selection corresponding to each distance (f: far; c: close to permanent watering point) of each paddock (1, 2, 3). Bars indicate 1 standard error. Numbers indicate the relative proportion of shrub patches to the pattern assessed by NLV. Different lowercase letters indicate significant differences in average grain among distance, paddock combinations.

differed between sites near and far from the watering points with contrasting grains of heterogeneity (Fig. 3). Coarse-grained sites showed high floristic similarity among them (i.e. low Euclidean distance). In contrast, we found larger differences in the floristic composition among fine-grained sites relative to coarse-grained sites (high and variable Euclidean distance). *Larrea divaricata* dominated at coarse-grained sites while fine-grained sites were dominated by different shrub species. In the paddock 1 (F1 in Table 1), the dominant species were *Chuquiraga avellanadae* and *Nassauvia fuegiana*, while *Atriplex lampa* and *Chuquiraga hystrix* dominated in the rest of the paddocks (F2 and F3 in Table 1).

Perennial grass cover was lower in coarse-grained sites than in fine-grained sites ($Z = 2.205$, $p = 0.013$; $Z = 1.712$, $p = 0.043$; $Z = 2.429$, $p = 0.007$, for paddocks 1, 2, and 3 respectively, Fig. 4a). This reduction in perennial grass cover was associated with low grass density (Fig. 4b) in paddocks 1 and 3 ($Z = 2.532$, $p = 0.005$; $Z = 2.170$, $p = 0.014$, respectively) and low MID (Fig. 4c) in paddocks 2 and 3 ($Z = 2.318$, $p = 0.010$; $Z = 2.123$, $p = 0.016$, respectively). The percentage of grazed perennial grasses did not vary significantly between sites (Fig. 4d). However, the grazed-grass cover was greater in fine-grained sites than in coarse-grained sites ($Z = 2.439$, $p = 0.007$; $Z = 1.898$, $p = 0.028$; $Z = 2.088$, $p = 0.018$, for paddocks 1, 2 and 3 respectively, Fig. 4e).

Analysis of spatial association between grasses and shrub patches

We found that total perennial grasses were indifferently distributed in relation to shrub patches in most transects and block sizes at both coarse and fine grain sites (Fig. 5a–b). However, in about one third of transects and at block sizes between 0.5 and 3 m, we found a positive association (aggregation) between perennial grasses and shrub patches at both fine- and coarse-grained sites. Negative associations (segregation) were infrequent throughout the range of distances analysed at both, fine and coarse-grained sites. Grazed perennial grasses were indifferently distributed in relation to shrub patches in most cases (Fig. 5c–d), although, we also found some cases of aggregation and segregation. In contrast, non-grazed grasses were frequently positively associated with shrub patches (Fig. 5e–f). Positive and negative associations were not related to transect orientation (data not shown).

The intensity of the association between perennial grasses and shrub patches evaluated by 3TLQC varied between fine and coarse-grained sites (Fig. 6a). It was significantly ($p < 0.05$) greater in fine-grained sites than

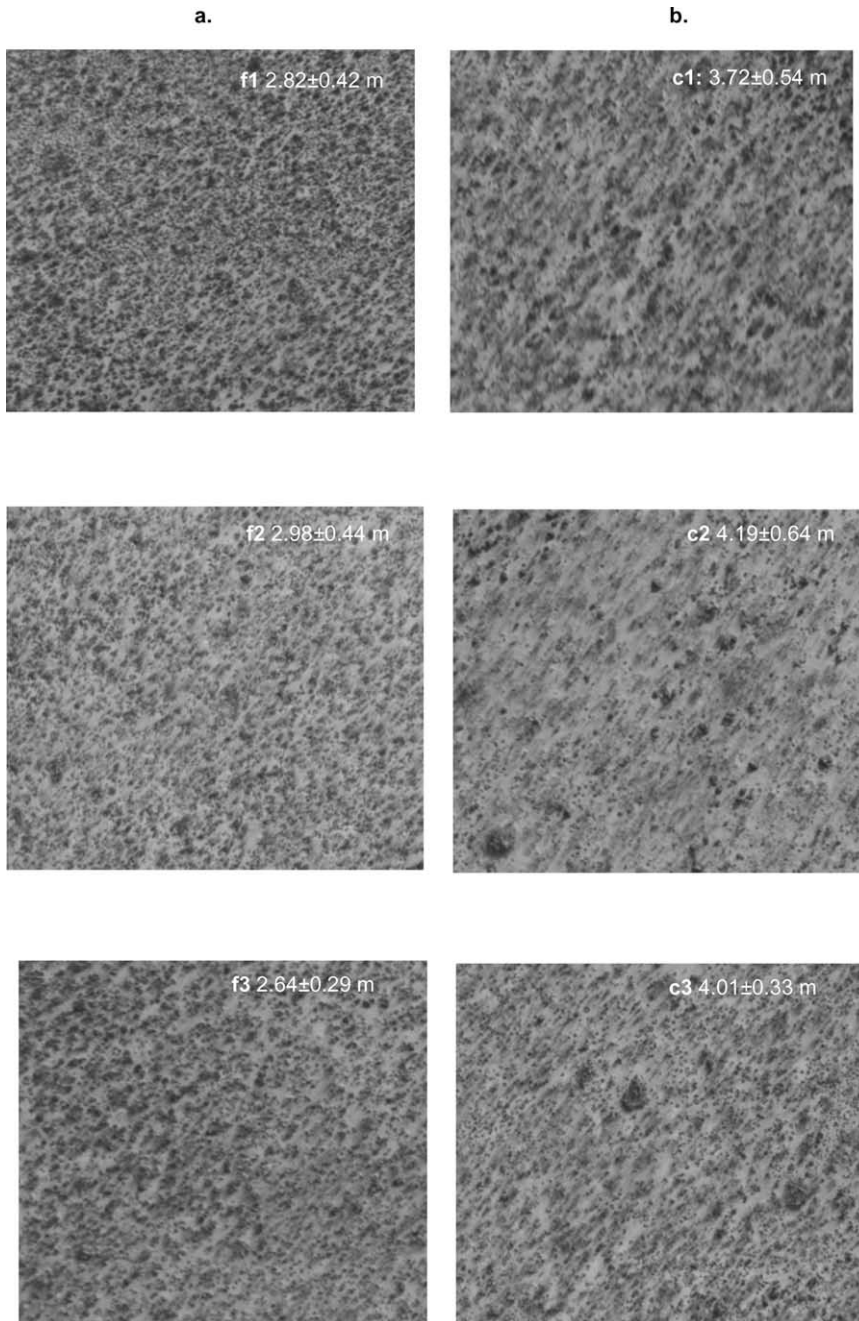


Fig. 2. Windows of aerial photographs selected as field sampling sites at paddocks 1, 2, 3 and their respective grain (scale of patchiness) (mean \pm standard error) of sites far: f (a) and close: c (b) to the watering point.

in coarse-grained sites, and the highest intensity values were found at small block sizes in fine-grained sites (Fig. 6a). The intensity of the association between grazed perennial grasses and shrub patches did not significantly ($p < 0.05$) differ between fine and coarse sites (Fig. 6b). In contrast, the intensity of the association between non-grazed grasses and shrub patches was higher in fine-grained sites than in coarse-grained sites throughout the range of block sizes analysed (Fig. 6c).

Discussion

Grazing affected the spatial structure of plant communities inducing not only spatial changes in the plant matrix related to the creation of “fertility islands” (shrub patches) but also in the structure and spatial patterning of perennial grass populations and grazing. As in other ecosystems, where the replacement of grasses by shrubs takes place after grazing disturbance (Schlesinger et al. 1996), we found that early degradation triggered by

Table 1. Specific plant cover (%) of each site (grain: F=fine, C=coarse; paddock: 1, 2, 3). Numbers in bold are totals of the corresponding growth form. +: Specific plant cover <1%.

Species	F1	C1	F2	C2	F3	C3
Shrubs	18	19	27	10	24	14
<i>Atriplex lampa</i>	1	+	9	+	8	+
<i>Bougainvillea spinosa</i>	1	3	2	+	2	1
<i>Chuquiraga avellanadae</i>	7	2	+	1	+	1
<i>Chuquiraga hystrix</i>	4	4	9	1	7	3
<i>Cyclolepis genistoides</i>			1			+
<i>Junellia alatocarpa</i>	+					
<i>Larrea ameghinoi</i>	+					
<i>Larrea divaricata</i>	1	7	3	5	5	6
<i>Larrea nitida</i>	+	+	+			+
<i>Lycium chilense</i>	+	+	+	+	+	+
<i>Monttea aphylla</i>	+	+	+			
<i>Prosopidastrum globosum</i>	3	2	2	2	2	1
<i>Prosopis alpataco</i>	1	+	1	1	+	1
<i>Schinus johnstonii</i>	+	1	+	+	+	1
Dwarf shrubs	14	5	1	4	3	4
<i>Acantholippia seriphoides</i>	+	1		1	+	+
<i>Brachyclados</i> sp.		+				
<i>Fabiana peckii</i>	+					
<i>Junellia seriphoides</i>	+	1				+
<i>Nassauvia fuegiana</i>	14	3	1	3	3	4
<i>Tetraglochin caespitosum</i>	+				+	
Grasses	8	1	12	1	8	2
<i>Elymus</i> spp.					+	
<i>Poa ligularis</i>	1	+	1	+	1	1
<i>Stipa humilis</i>	+	1	+	+	+	1
<i>Stipa speciosa</i>	3	+	3	+	2	+
<i>Stipa tenuis</i>	4	+	8	1	5	+
<i>Stipa neaei</i>	+					
Total	40	25	40	15	35	20

grazing resulted in an increase of the vegetation grain size (Figs 1 and 2). At coarse-grained sites both shrub patches and bare soil areas were larger than those of fine grained sites (Figs 1 and 2), while shrub cover was lower (Table 1), suggesting that the internal cover of shrub patches was lower at these intensely grazed areas, in agreement with results of Bisigato and Bertiller (1997). In our study, we found that the increase in the scale of patchiness was related to floristic and structural changes and reduced species richness (Table 1). This is also

consistent with other studies reporting low species richness under heavy grazing (Cid and Brizuela 1998, Fuhlendorf and Smeins 1999). Floristic changes in the dominant shrubs, however, were not directly related to the increase in the grain size (Fig. 1), since grain size only depends on the density of patches and is independent of patch size. However, replacement among shrub species could be related to the size of the shrub phase, since individuals of *L. divaricata* have larger crown diameters than individuals of *Atriplex lampa* or *Chuquiraga* spp. Accordingly, Adler et al. (2001) suggested that increased grain size occurs when the vegetation structure and its floristic composition are modified as a consequence of grazing. Changes such as increasing patch fragmentation, decreasing patch number and connectivity, as previously reported for grazed paddocks at different Patagonian ecosystems, may also account for the coarse-grained pattern in sites near watering points (Bisigato and Bertiller 1997, Bertiller et al. 2002b).

Changes in the overall scale of patchiness were associated with reduction in perennial grass cover as a consequence of reduced density and/or size of grass bunches (Fig. 4a–c) but these did not affect the overall spatial distribution of perennial grasses in relation to shrub patches (Fig. 5a–b). At both fine and coarse-grained sites, perennial grasses were mostly indifferently distributed with respect to shrub patches and we did not

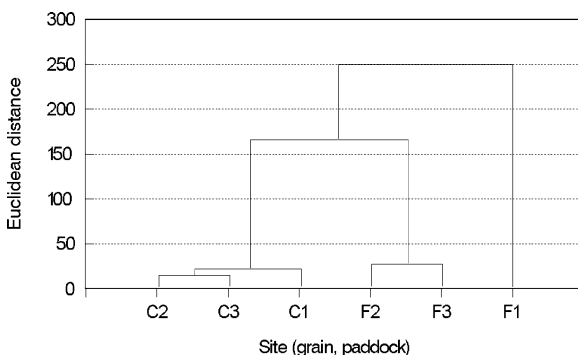


Fig. 3. Dendrogram using average linkage and Euclidean distances as indicator of floristic similarity among areas. C: coarse grain size, F: fine grain size in paddocks 1, 2, and 3.

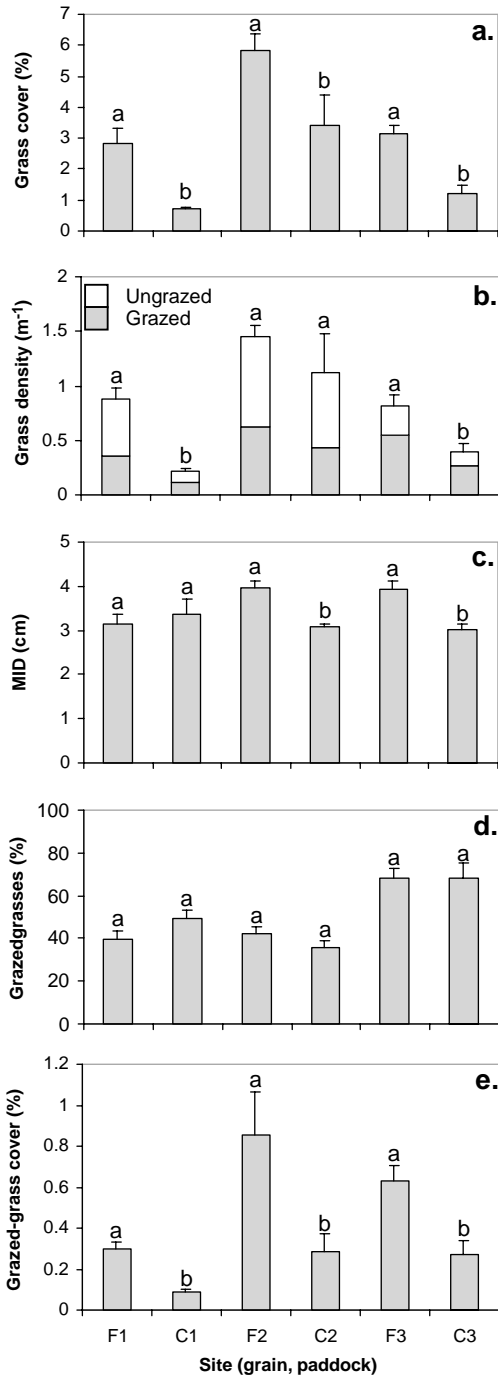
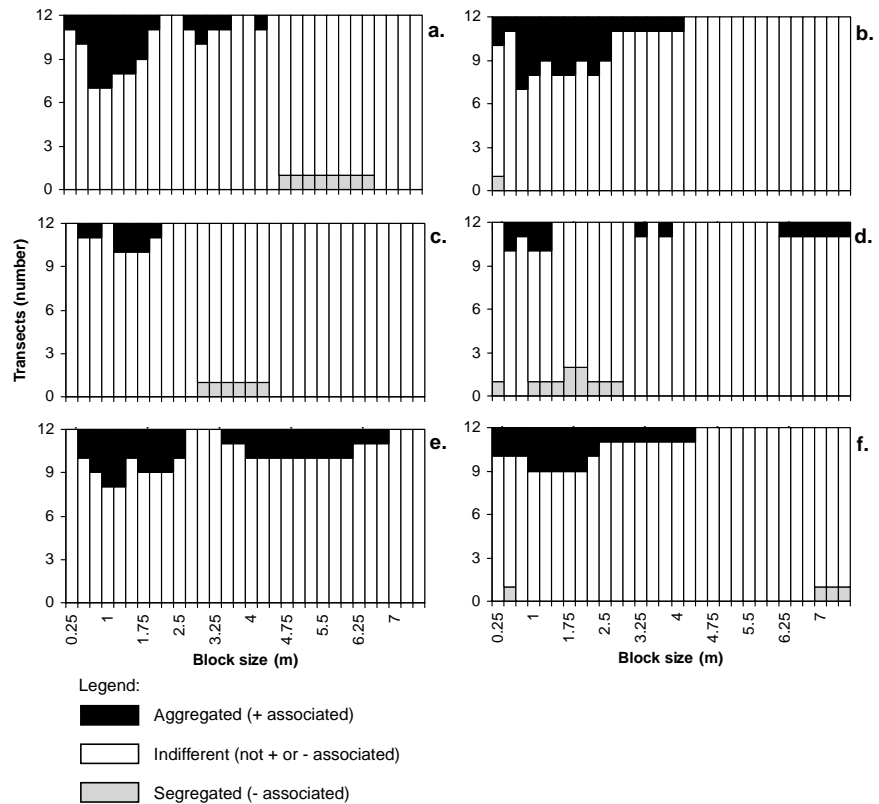


Fig. 4. Grass cover (a), grass density (b), mean intercepted diameter (MID) of grasses (c), proportion of grasses grazed (d), and grazed-grass cover at each area (e). Bars indicate 1 standard error. Acronyms as in Fig. 3. Different lowercase letters indicate significant differences among areas within a paddock.

find changes in the relative importance of segregation and aggregation between shrubs and grasses across the piosphere that would indicate shifts in the facilitation/competence balance. The low aggregation between

grasses and shrub patches may also be an indirect evidence of the low effect of trampling on the spatial patterning of grasses across the piosphere. Sheep trails usually sort shrub patches, which are greater than sheep body size indicating that trampling mostly occurs in the bare soil. Despite this, we found, as in other arid ecosystems (Belsky 1998, Aguiar and Sala 1999), some cases of positive association between perennial grasses and shrub patches which were not related to directionality or anisotropy in the establishment and/or survival of grasses. This could be the consequence of two different but not exclusive processes: greater establishment of grasses in the neighbourhood of plant patches, and higher survival in protected microsites inside patches. In relation to the first process, Bisigato and Bertiller (2004a) found greater grass seedling establishment at the periphery of plant patches than in bare soil areas. The concentration of grasses at the periphery of shrub patches may result from resource accumulation such as seeds and nutrients (Bertiller 1998, Guo et al. 1998, Facelli and Brock 2000) and/or from an ameliorated microclimate (Belsky et al. 1989, Bertiller et al. 2002a) at these microsites that would improve seedling emergence and establishment (O'Connor and Everson 1998). In relation to the second process, higher seedling survival at protected microsites within patches than at inter-patch areas may lead to the aggregation between non-grazed grasses and shrub patches observed in our study sites (Fig. 5e-f). This suggests that at both fine- and coarse-grained sites shrub patches could in part protect both seedlings and adults of grasses from herbivores due to anti-herbivore defences like spines (Lauenroth 1998, Milchunas and Noy-Meir 2002) and/or another deterrent structures (e.g. resinous leaves) with low N concentration and/or high concentration of secondary metabolites (del Valle and Rosell 1999, Carrera et al. 2003). Such refuges may have important effects on plant communities providing mechanisms of resistance to grazing that eventually improve plant richness (Milchunas and Noy-Meir 2002) and contribute to increase grass densities near shrub patches. In this sense, the intensity of association between shrub patches and non-grazed grasses was significantly greater in fine-grained sites than in coarse-grained sites (Fig. 6c) probably due to higher concentration of grasses near shrub patches with dense canopies relative to those with more open canopies. This may be related to floristic changes along the piosphere (Table 1). Grazing lead to the replacement of *Atriplex lampa* or species of the genus *Chuquiraga* with dense canopies by *L. divaricata* with more open canopies. In consequence, patches near watering points with low internal cover may exert less-efficient anti-herbivore protection than better preserved shrub patches far away from watering points (O'Connor 1991).

Fig. 5. Number of transects ($n = 12$; 4 transect/site \times 3 sites/grain) with significant aggregation or segregation at each block size evaluated by 3TLQC. Association between total grasses and shrub patches at fine-grained sites (a), total grasses and shrub patches at coarse-grained sites (b), grazed grasses and shrub patches at fine-grained sites (c), grazed grasses and shrub patches at coarse-grained sites (d), non-grazed grasses and shrub patches at fine-grained sites (e), and non-grazed grasses and shrub patches at coarse-grained sites (f).



Contrarily to our expectations, grazed grasses were to a great extent homogeneously distributed with respect to shrub patches at both fine- and coarse-grained sites (Fig. 5c–d). Our results agree with those of Wallis de Vries and Schippers (1994), reporting that free-ranging cattle may display high selectivity of foraging sites at macro level (i.e. high and low grazing pressure sites at the paddock level), but random occupancy of vegetation units (randomness in the distribution of grazed perennial grasses at the patch level). Likewise, Bailey et al. (1996) found that relationships between abiotic factors (such as distance to water) and the patterns of grazing use are usually stronger and more predictable than relationships between grazing and biotic factors (e.g. forage quality and quantity). In contrast, in more humid ecosystems the greatest variation in grazing impact was found at small scales (Palmer et al. 2003). Adler et al. (2001) proposed that the resulting spatial organization of grazed communities could be quite different depending on the relative scales of plant heterogeneity and grazing. The proportion of grazed perennial grasses did not differ between sites with contrasting grain size (Fig. 4d). However, as a consequence of greater grass cover at fine-grained sites than at coarse-grained sites, the cover of grazed grasses was also greater in the former (Fig. 4e). This suggests that in paddocks with piosphere formation around permanent watering points (Jeltsch et al. 1997),

fine-grained sites (distant from watering points) are more important as feeding stations than coarse-grained sites near watering points. The consequences of this differential use could lead to degradation of fine-grained sites and to higher homogeneity in spatial plant structure and floristic composition within paddocks with respect to the condition observed at present, increasing the size of the highly degraded zone within the piosphere. In this sense, Jeltsch et al. (1997) and Weber et al. (2000), using grid-based simulation models, found that the piosphere zones expand outwards at a rate correlated with the grazing pressure. In contrast to shrubs, we did not expect that changes in floristic composition of grasses (Table 1) could have exerted a major influence in their spatial and grazing patterning since an important number of structural and functional attributes are more homogeneous in grasses than in shrubs (Bertiller et al. 1991, 2005, Bisigato and Bertiller 1997, Bisigato et al. 2002, Carrera et al. 2003). Possible influences of grass species traits on their spatial patterning are the target of our continuing research.

In summary, our results show that a feedback exists between the spatial distribution of species preferred by grazers and the spatial patterning of use of these species. In sites with dense and conserved shrub patches, these latter constitute more effective anti-herbivore defences that would protect grass populations from grazing than

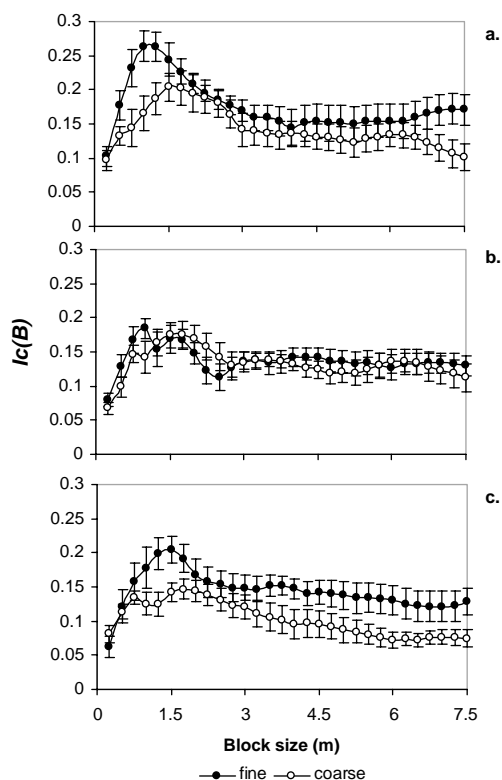


Fig. 6. Intensity of association ($I_c(B)$) between total grasses and shrub patches (a), grazed grasses and shrub patches (b) and non-grazed grasses and shrub patches (c) at different lags. Bars indicate ± 1 standard error.

in degraded sites. On the other hand, less impacted grass populations such as those observed in fine-grained sites, are denser and with larger bunches in comparison with those found at coarse-grained sites. Thus, the spatial patterning of non-grazed and grazed grasses could be an important tool to characterize the grazing behaviour of grazers and its further consequences for plant dynamics (Hester and Baillie 1998, Weber et al. 2000, Oom et al. 2002). Usually, management recommendations to fit stocking rates are based on the botanical composition of grazed communities, without taking into consideration the spatial patterning of vegetation (Roguet et al. 1998). This knowledge could be of use to the development of indicators of the state of conservation of natural ecosystems and in the evaluation of early desertification signs. Also, the assessment of the spatial patterning of vegetation would provide valuable information related to the distribution of soil resources (Schlesinger et al. 1996, Bhark and Small 2003, Carrera et al. 2003) as well as clues for vegetation functioning (Wu et al. 2000). Particularly, the assessment of the effects of changes in the spatial arrangement of shrub patches on the susceptibility of grasses to be grazed is quite relevant

in the detection of degradation thresholds useful for the development of sustainable management practices.

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