

Spatial heterogeneity at different grain sizes in grazed *versus* ungrazed sites of the Patagonian steppe¹

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Abstract: In arid ecosystems, grazing-induced desertification can be either associated with an increase or a decrease in the spatial heterogeneity of plant communities. We explored the grazing-associated change in the spatial heterogeneity along a gradient of plot sizes (= grains) in a Patagonian steppe with two structural phases: scattered grasses and shrubs surrounded by grasses. We compared the biomass heterogeneity (estimated from locally calibrated digital photographs) of three sites: one ungrazed for the last 26 y and two moderately grazed. On each site, we analyzed three belt transects of 50 contiguous 20- × 20-cm plots and grouped the photographs into plots of increasing size. We used the *p* parameter (gamma distribution) to measure the global heterogeneity of the biomass and semivariograms to calculate internal heterogeneity and spatial dependence (estimated from the y-intercept and the fractal dimension of semivariograms, respectively). We found that the global and the internal heterogeneity were higher in the grazed sites than in the ungrazed one, possibly because grazing increases the contrast between the structural phases. However, the fractal dimension did not change with grazing. The difference between grazed and ungrazed sites did not disappear when grain increased, probably because the grazing-induced biomass increase of the shrub-dominated phase was higher than the biomass decrease of the scattered grasses phase.

Keywords: arid ecosystems, biomass, desertification, fractal dimension, semivariogram.

Résumé : Dans les écosystèmes arides, la désertification causée par le pâturage des animaux domestiques peut être associée à des augmentations ou des diminutions de l'hétérogénéité de la végétation. Nous avons exploré le changement de l'hétérogénéité spatiale associée au pâturage le long d'un gradient de taille de parcelles. Nous avons réalisé cette étude dans une communauté végétale de la Patagonie avec deux phases structurales, soit celle avec une population de graminées dispersées et celle avec des arbustes entourés de graminées. Nous avons comparé l'hétérogénéité de la biomasse de trois sites à l'aide de photographies numériques. L'accès à l'un des sites a été interdit aux animaux pendant 26 ans. Dans les deux autres sites, un nombre modéré d'animaux ont pu paître. Dans chaque site, nous avons suivi trois transects, composés de 50 parcelles contiguës de 20 × 20 cm chacune. Nous avons groupé les photographies de ces parcelles en ensembles de taille croissante. Nous avons utilisé le paramètre *p* de la distribution gamma pour mesurer l'hétérogénéité générale de la biomasse, et des semivariogrammes pour mesurer l'hétérogénéité intrinsèque et la dépendance spatiale (estimées respectivement à partir de l'ordonnée à l'origine et de la dimension fractale des semivariogrammes). Les hétérogénéités générale et intrinsèque sont plus grandes dans les sites pâturés que dans le site sans animaux, probablement parce que le pâturage augmente le contraste entre les deux phases structurales de végétation. Cependant, la dimension fractale ne change pas avec le pâturage. La différence entre les sites pâturés et celui sans animaux ne disparaît pas à mesure que la taille des parcelles augmente, probablement parce que l'augmentation de la biomasse provoquée par le pâturage dans la phase structurale dominée par les arbustes est plus grande que la diminution de la biomasse dans la phase structurale avec graminées.

Mots-clés : biomasse, désertification, dimension fractale, écosystèmes arides, semivariogrammes.

Nomenclature: Correa, 1971-1984.

Introduction

In arid and semi-arid ecosystems, grazing-induced desertification processes are often associated with an increase in the spatial heterogeneity of both the plant community structure and the distribution of soil resources (Schlesinger *et al.*, 1990; Aguiar & Sala, 1999). However, in some of these ecosystems, grazing reduces the spatial heterogeneity (Adler, Raff & Lauenroth, 2001). A recent theoretical development suggests that in ecosystems where

herbivores are selective, spatial heterogeneity will increase if grazing increases the contrast among the different structural phases of the community, whereas the effect will be the opposite if grazing decreases the contrast among structural phases (Adler, Raff & Lauenroth, 2001). In addition, as animal selectivity decreases when stocking rate increases (Vallentine, 2001), heterogeneity increases with grazing at moderate stocking rates, but decreases at very high stocking rates (Cid & Brizuela, 1998).

Scale issues are critical in analyses of the consequences of grazing on spatial heterogeneity (Senft *et al.*, 1987). The spatial scale of observation needs to be care-

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fully defined. Such definition includes three elements: a) the extent of the area under study, b) the distance among the sampling units, and c) the size of each sampling unit (grain; Legendre & Legendre, 1998). When grain size increases, heterogeneity within plots must increase and heterogeneity between plots must decrease, because the larger the plots are the higher the probability of including the different structural phases of the community (Wiens, 1989). Similarly, the effect of distance on spatial heterogeneity can be subdivided into two terms: the "internal heterogeneity" and the "spatial dependence". The former corresponds to the heterogeneity found at distances smaller than the minimum distance between plots (nugget effect; Ryel, Caldwell & Manwaring, 1996). The latter corresponds to variation of spatial heterogeneity as a function of distance between plots (Dale, 1999). Several authors have studied the structural change of plant communities along a gradient of grains (Greig-Smith, 1952). Other authors have studied the structural variation of plant communities among plots located at increasing distances (Augustine, 2003) or subjected to different grazing intensities (Adler & Lauenroth, 2001). However, no study has analyzed the variation of the spatial heterogeneity of plant communities subjected to different grazing intensities when both grain size and distance among plots increase.

The aim of this work is to analyze how the spatial heterogeneity, the internal heterogeneity, and the spatial dependence of a Patagonian steppe change with grain size in grazed *versus* ungrazed sites. The shrub-grass steppe in the southwest of Chubut (Patagonia) is an interesting ecosystem in which to explore this issue, because it has a strong and well-studied spatial pattern composed of two different structural phases: shrubs surrounded by grasses and scattered grasses (Aguilar & Sala, 1999). Taking into account that sheep prefer grasses to shrubs (Soriano, 1956), we predict that grazing at moderate stocking rates could result in a large differentiation among phases because grazing pressure on each one should be different. In addition, the two structural phases can be differentially affected by seed and resource dynamics. Water and wind erosion transform the scattered-grasses phase into a source of seeds and soil resources, which are accumulated in the sink shrub-plus-grasses phase (Aguilar & Sala, 1999). The biomass loss of the scattered-grasses phase leads to a liberation of soil resources that extensive and deep roots of shrubs could eventually reach (Fernández & Paruelo, 1988).

Our research evaluated change of biomass spatial heterogeneity along a gradient of grain size in one site ungrazed for the last 26 y and two moderately grazed sites. The theoretical framework proposed by Adler, Raff, and Lauenroth (2001) let us infer the following two hypotheses: 1) spatial heterogeneity of the biomass will be higher in the moderately grazed sites than in the ungrazed site, because grazing will reduce the biomass in grass-dominated patches more than in shrub-dominated patches; and 2) if grazing-induced reduction of grass biomass is strictly compensated for by an increase of the shrub biomass, grazed and ungrazed plots will tend to have the same biomass as grain increases. Then, differences in the

spatial heterogeneity among grazing situations will tend to disappear along this grain gradient.

Methods

SITE DESCRIPTION

The study was conducted at the experimental field of INTA (Instituto Nacional de Tecnología Agropecuaria) at Río Mayo, in the southwest part of Chubut Province (45° 41' s, 70° 16' w), in typical shrub-grass steppes of the Patagonian Occidental District (Soriano, 1956). This district takes up about 30% of the Patagonian Phytogeographic Province (León *et al.*, 1998). The dominant plant community in the area is that of *Stipa speciosa*, *Adesmia campestris*, *Berberis heterophylla*, and *Poa lanuginosa* (Golluscio, León & Perelman, 1982). The dominant shrub species are *Mulinum spinosum*, *Adesmia campestris*, and *Senecio filaginoides*, and the dominant grasses are *Stipa speciosa*, *Stipa humilis*, and *Poa ligularis*. Annual and perennial herbs account for only 3% of plant cover (Golluscio, León & Perelman, 1982). The average annual precipitation is 137 mm, and 70% falls in autumn-winter, when mean monthly temperature varies from 2 to 7 °C (Sala *et al.*, 1989).

EXPERIMENTAL LAYOUT

Measurements were made in January 1999 (summer) in three field sites: one ungrazed for the last 26 y (UG) and two others (G1 and G2), located near the enclosure, grazed almost year-round since 1947 with a moderate stocking rate of 0.3 sheep·ha⁻¹, which corresponds to the average for the area. Before 1947 all of the farm was subjected to a stocking rate higher than the current one (A. Soriano, pers. comm.). The ungrazed site may still bear the impact of the earlier sheep grazing because large herbivores have been excluded by fencing only since 1973. As our ungrazed treatment did not have true replications, statistical differences among sites were not automatically interpreted as grazing consequences (Hurlbert, 1984). However, the three sites corresponded to the same plant community (Golluscio, León & Perelman, 1982) and had the same grazing history because they were located on the same paddock. This suggests that differences found among them in spatial heterogeneity can be reasonably attributed to the effects of grazing. However, as the ungrazed treatment does not have true replications, our results should not be extrapolated to other Patagonian steppes (Hurlbert, 1984).

Biomass was estimated from the Green Pixels Percentage (GPP) in digital photographs. This approach produces very accurate correlations, although valid only locally, with both biomass and cover estimations (Richardson, Karcher & Purcell, 2001). In each site, three parallel belt transects of 10 × 0.2 m, with a distance of 10 m between them, were located in a randomly selected area, edaphically and topographically homogeneous. On each transect, 50 digital photographs of 20 × 20 cm were taken with a Sony Mavica MVC-FD7 camera (Sony Corporation, Tokyo, Japan) with a resolution of 640 × 480 pixels. To outline the plots, 10 contiguous metal frames of 0.2 × 1 m, subdivided into five plots of 20 × 20 cm

each, were located over each transect. Finally, the biomass of 10 20- 20-cm plots, the first of each frame, was harvested on each transect to evaluate the method.

The MGPIXEL software (Paruelo, Lauenroth & Roset, 2000) was applied to calculate the Green Pixel Percentage (GPP) of each 20 20 cm plot. Additionally, the qualitative abundance-cover scale of Braun-Blanquet (1932) was used to estimate the cover of grasses, shrubs, and herbs of each plot. The harvested biomass was separated into the green and standing dead fractions for grasses, shrubs, and annual plus perennial herbs. The different fractions were oven dried at 80 °C to constant weight (72 h) and then weighed with a digital Mettler Toledo PB 33 balance (± 0.1 mg).

METHODOLOGICAL APPROACH

We used the p parameter (mean²·variance⁻¹) of the gamma distribution (Tsutsumi *et al.*, 2000) to characterize the global spatial heterogeneity of vegetation, and semivariograms (Palmer, 1988) to characterize the internal heterogeneity and spatial dependence. The frequency distribution of biomass per area unit fits a gamma distribution. A p -value equal to 1 indicates a random spatial distribution of biomass, a $p < 1$ heterogeneous distribution, and a $p > 1$ homogeneous distribution (Tsutsumi *et al.*, 2000). Semivariograms are graphs of the variability among plots as a function of the distance between them. The parameter used to measure such variability was the semivariance (Palmer, 1988) of the Green Pixel Percentage (GPP):

$$\gamma(h) = \frac{\sum_{i=1}^{N(h)} [GPP_i - GPP_{i+h}]^2}{2N(h)} \quad [1]$$

where $\gamma(h)$ = semivariance of a set of samples separated by a distance h , GPP_i = green pixel percentage of i plot, GPP_{i+h} = GPP of a plot located at a distance h from plot i , and $N(h)$ = number of plot pairs separated by a distance h .

Semivariograms can have diverse forms. When they are horizontal (slope = 0), the system is equally homogeneous (or heterogeneous) for all the distances considered, indicating spatial independence and lack of autocorrelation. When the semivariance increases proportionally with distance (slope > 0), the system becomes more heterogeneous as distance among plots increases, indicating spatial dependence and autocorrelation (Palmer, 1988). The variability at a distance shorter than the minimum sampled is the internal spatial heterogeneity and is represented by the y-intercept of the semivariance *versus* distance model (nugget semivariance; Ryel, Caldwell & Manwaring, 1996). The fractal dimension of the semivariograms synthesizes information about the spatial dependence (*i.e.*, variation of vegetation heterogeneity with distance among samples). It can be obtained from the slope of the log/log regression between the semivariance and the distance among samples (Equation 2; Palmer, 1988):

$$D = \frac{(4 - m)}{2} \quad [2]$$

where D = fractal dimension of a semivariogram, and m = slope of the log/log regression between the semivari-

ance [$\gamma(h)$] and the distance among samples (h).

The previous equation shows that when heterogeneity is constant at all distances, the fractal dimension tends to 2 ($m = 0$) and when heterogeneity increases with distance, the fractal dimension tends to 1 ($m = 2$).

DATA ANALYSIS

To test the suitability of GPP as an estimator of the amount of vegetation in each photo, we performed multiple linear regressions between the GPP and both the cover or the biomass of each community component. To evaluate whether the three sites differed significantly in their physiognomy, we compared the cover of the different community components by ANOVA tests among sites (three treatments), considering transects as within-site replications (*i.e.*, 3 replications·treatment⁻¹) (Steel & Torrie, 1980).

To construct the grain gradient, we developed a method that uses transects subdivided into a decreasing number of plots of increasing size. Within the nine 10-0.2-m transects, we used five plot sizes (grains): single photos (50 plots of 20 20 cm) and groups of two contiguous photos (25 plots of 40 20 cm), five contiguous photos (10 plots of 100 20 cm), 10 contiguous photos (five plots of 200 20 cm), and 25 contiguous photos (two plots of 500 20 cm). This gradient of grains encompassed the size of the shrub-plus-grasses structural phase. The diameter of shrubs found along the nine lines was 60.1 ± 3.6 cm (mean ± SE, $n = 29$), and the diameter of grasses was 15.7 ± 1.2 cm (three species in three sites; M. I. Nogués Loza, unpubl. data). For the smallest grain size there were 50 points per replication, 150 points per site, and 3,675 total pairs per site. This number of points per site is comparable to those of previously published papers (Jackson & Caldwell, 1993: 362 points per site; Schlesinger *et al.*, 1996: 109 points per site; Ryel, Caldwell & Manwaring, 1996: 150 points per site). However, we had a lower number of pairs per site because our experimental layout emphasized the need for replication within sites, which was absent in the cited studies.

For each grain and transect, we calculated the p parameter, the semivariance [$\gamma(h)$] (equation [1]), the y-intercept of the regression between semivariance and distance among plots, and the fractal dimension (D) (equation [2]). To construct the semivariograms we only considered a) distances among plots " 5 m, because at greater distances the low number of plot pairs made semivariance estimations erratic and unreliable (Palmer, 1988), and b) grains " 1 m, because the number of plot pairs also decreases dramatically when plot size increases. For each of the grains, we analyzed the semivariations with a two-way ANOVA of three sites \times n distances among plots. The number of distances decreased with grain: 25 for 20 20 cm plots, 12 for 20 40 cm plots, and five for 20 100 cm plots.

To test the two hypotheses of this paper we used a one-way ANOVA among sites (three replications per site) with a repeated-measures design to evaluate the effect of the different grains. The response variables were the p parameter and the y-intercept and fractal dimension of the semivariograms. The analysis of the site effects allowed us to explore hypothesis 1, and the analysis of the site

grain interaction effect, hypothesis 2. In order to characterize differences among sites, we used orthogonal contrasts comparing ungrazed *versus* grazed sites (UG *versus* G) and between grazed sites (G1 *versus* G2) (Steel & Torrie, 1980). To analyze the effect of grain, we performed linear orthogonal contrasts assigning increasing linear coefficients to plots of increasing size. The distribution of data subjected to ANOVA was normal (Shapiro-Wilks test), and their variances were homogeneous (Bartlett test). We made semivariograms using Excel (Microsoft, 1997) and conducted statistical analysis using Statistica (StatSoft, 1995). Differences were considered statistically significant when $P < 0.05$.

Results

The green pixel percentage (GPP) was a good estimator of both green biomass and total cover ($P < 0.01$, Table I). In both cases, correlations were better explained by shrubs than by grasses, probably because of the higher summer phenological activity of shrubs (Golluscio, Oesterheld & Aguiar, in press).

The physiognomy of the 26-y-ungrazed and grazed sites was not different ($P < 0.05$). There were no significant differences between the two types of site in any component of the community. However, there were significant differences between the two grazed sites in terms of grass- and total- cover ($G2 > G1$) (Table II).

The ungrazed site had lower global (distance-independent) spatial heterogeneity (higher p) than the grazed sites (with G1 more heterogeneous than G2). In addition, heterogeneity decreased as grain increased (F of the linear orthogonal contrast among grains = 55.65, $P < 0.01$), without any grain site interaction (Figure 1).

For the three smallest grains, the semivariance was greater in the grazed sites than in the ungrazed site for all distances among plots, with no significant differences

TABLE I. Multiple linear regressions among the Green Pixel Percentage (GPP) and the different fractions of green biomass ($n = 150$) and cover ($n = 450$). Symbols represent the statistical significance of the y-intercept, the partial slopes (both compared against zero), and the overall regression model: ** = $P < 0.01$, * = $0.01 < P < 0.05$, ns = $P > 0.05$.

Independent variable	y-intercept	Partial slopes			Determination coefficient (r^2)
		Shrubs	Grasses	Herbs	
Biomass	4.18 **	2.1 **	0.14 ns	3.31 ns	0.47 **
Cover	4.03 **	0.3 **	0.07 **	0.15 ns	0.45 **

TABLE II. Different structural components of the cover at the three analyzed sites (UG = Ungrazed, G1 = Grazed 1, G2 = Grazed 2). The mean \pm SE of the three 10-m transects is indicated. For each fraction, different letters indicate significant differences among sites (ANOVA with orthogonal contrasts on arc-sine square-root-transformed data, $P < 0.05$).

Site	Grasses	Shrubs	Herbs	Total
UG	15.46 \pm 2.40 ^{ab}	3.10 \pm 1.40 ^a	0.20 \pm 0.20 ^a	18.77 \pm 2.64 ^{ab}
G1	11.13 \pm 0.86 ^a	7.32 \pm 2.28 ^a	0.09 \pm 0.04 ^a	18.54 \pm 2.83 ^a
G2	24.87 \pm 2.19 ^b	6.98 \pm 2.19 ^a	0.00 \pm 0.00 ^a	31.84 \pm 4.06 ^b

among distances and no site distance interaction (ANOVA test, Table III) (Figure 2). Contrary to p , G2 was more heterogeneous than G1, probably because of the influence of the mean on p (mean GPP was 10.9% for G2 and 4.6% for G1).

Internal heterogeneity, given by the y-intercept of the regression $\gamma(h) = f(h)$, was lower in the ungrazed site than in the grazed sites for all grains (with $G2 > G1$) and decreased significantly as grain increased (F of the linear orthogonal contrast among grains = 36.1, $P < 0.01$), without any site grain interaction (Figure 3a). Fractal dimension varied between 1.7 and 1.9 for all the situations, and this variation was not associated with sites or grains (Figure 3b).

Discussion

Overall, the results were consistent with our first hypothesis (moderate grazing may induce an increase in spatial heterogeneity): grazed sites had higher global spatial heterogeneity (Figure 1) and internal heterogeneity (Figures 2a and 3a). However, they did not differ in spatial dependence, at least within grains > 1 m (Figure 3b). This hypothesis was in agreement with the general model of Adler, Raff, and Lauenroth (2001). Sheep have a

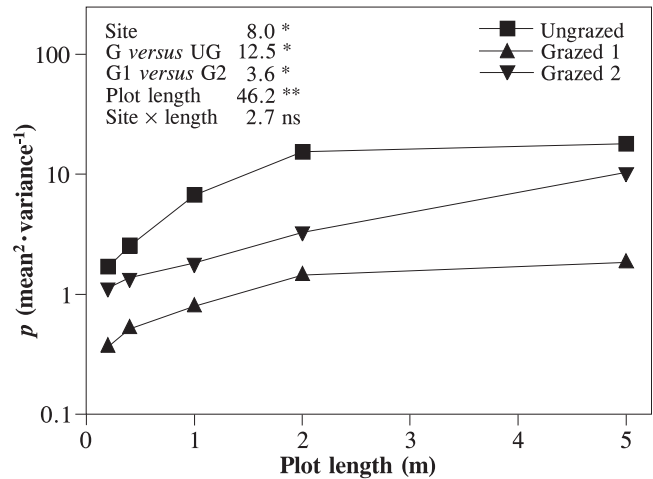


FIGURE 1. Variation of the global spatial heterogeneity, estimated from the p parameter of the gamma distribution ($\text{mean}^2 \cdot \text{variance}^{-1}$), as a function of plot length for the three sites (mean values of three transects for each site). ANOVA results, performed on the log-transformed data, are summarized to differentiate the effects of site and plot length (F values; ** = $P < 0.01$, * = $0.01 < P < 0.05$, ns = $P > 0.05$).

TABLE III. F values of the site (G = Grazed, UG = Ungrazed) and distance effects on the semivariance (ANOVA with orthogonal contrasts on log-transformed data) at different plot sizes. Symbols indicate whether the effects are statistically significant (** = $P < 0.01$, * = $0.01 < P < 0.05$, n.s. = $P > 0.05$).

Effect	Plot size (cm)		
	20	20 40	20 100
Site	155.5 **	90.7 **	34.4 **
G <i>versus</i> UG	241.3 **	138.5 **	54.6 **
G1 <i>versus</i> G2	69.7 **	43.3 **	14.2 **
Distance	0.5 ns	0.4 ns	0.3 ns
Site distance	0.1 ns	0.2 ns	0.2 ns

selective grazing pattern (Hofmann, 1989), and at a moderate stocking rate they may exert a differential grazing pressure on the two structural phases of the plant community since they prefer grasses over shrubs (Soriano, 1956). Nevertheless, analysis of a wider grazing-intensity gradient probably would show smaller differences in the grazing pressure on the two structural phases.

In relation with our second hypothesis (differences in heterogeneity among sites may disappear as grain increases), differences in the global and internal heterogeneity between the grazed sites and the 26-y-ungrazed site remained statistically significant along the whole grain gradient, without significant grain site interactions (Figures 1 and 3a). This suggests that the expected biomass decrease in scattered grasses was not compensated

for by an equivalent biomass increase in the shrub-plus-grasses phase. However, two opposite causes could have produced this lack of compensation: the increase of the shrub-plus-grasses biomass might have been bigger or smaller than the decrease of the scattered grasses. The GPP/cover ratio of shrub-dominated over grass-dominated 20- 20-cm plots tended to be significantly higher in the grazed sites ($G1 = 1.73$ and $G2 = 1.07$) than in the ungrazed site ($UG = 0.52$) (ANOVA with orthogonal contrasts, $P = 0.069$). This indirect evidence suggests that, at least in these three sites of the Patagonian steppe, grazing would increase the rates of resource transfer from scattered grasses to shrub-plus-grasses phases, generating a biomass increase on the shrub-dominated phase.

Independently of the influence of grazing, the coexistence of high- and low-resource patches could enable stands to increase their primary production with respect to spatially homogeneous stands with the same mean precipitation (Aguiar & Sala, 1999). On the other hand, under constant precipitation, if grazing exerts an opposite effect on the different structural phases of the community, it can cause a null net change of production. This lack of response of primary production to grazing is frequently found in arid zones (Schlesinger *et al.*, 1990). Nevertheless, such compensation for the effects of grazing on different structural phases does not explain the

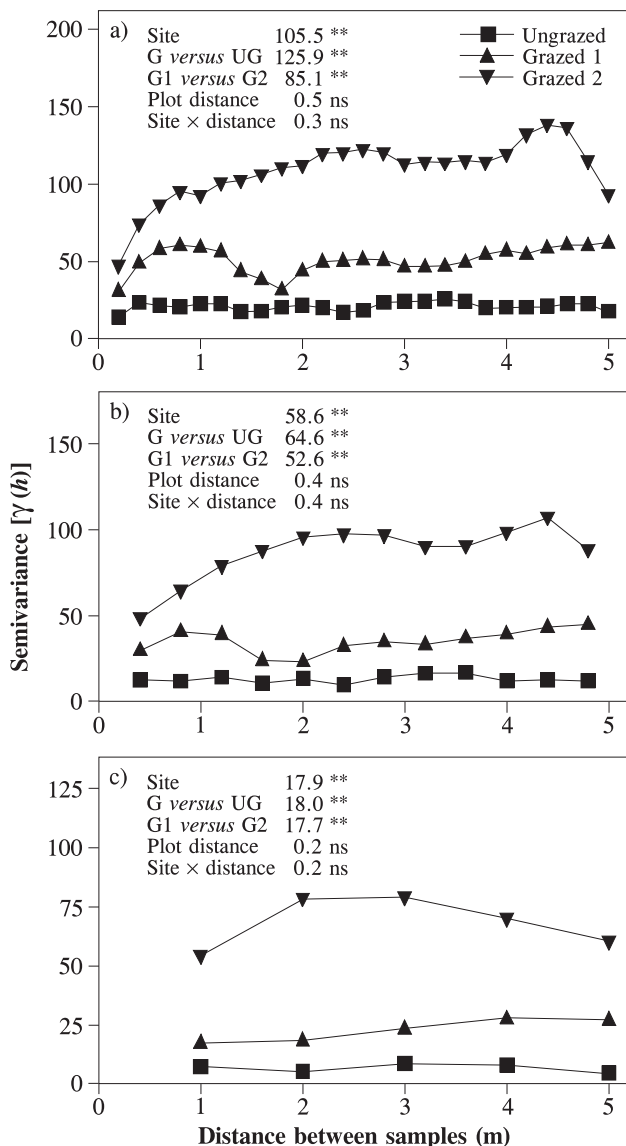


FIGURE 2. Variation of the semivariance as a function of the distance among plots for the three sites (mean values of three transects for each site), considering three plot lengths: a) 20 × 20 cm, b) 20 × 40 cm, and c) 20 × 100 cm. ANOVA results are summarized to differentiate the effects of site and distance among plots at each plot length (F -values; ** = $P < 0.01$, * = $0.01 < P < 0.05$, *n.s.* = $P > 0.05$).

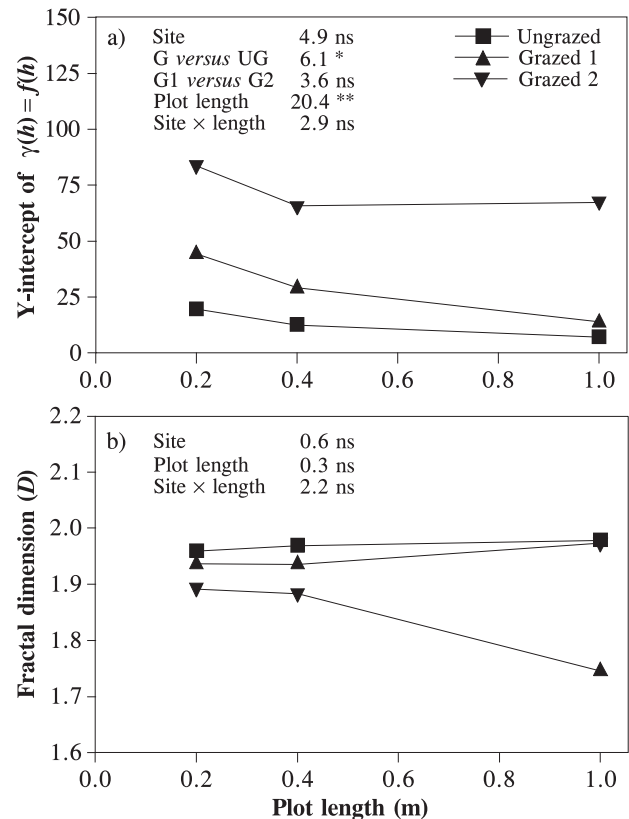


FIGURE 3. Variation of a) internal heterogeneity [= y-intercept of the regression $\gamma(h) = f(h)$], and b) fractal dimension (D) as a function of the plot length for the three sites (mean values of three transects for each site). ANOVA results of y-intercept (log transformed data) and D are summarized to differentiate the effects of site and plot length (F -values; ** = $P < 0.01$, * = $0.01 < P < 0.05$, *n.s.* = $P > 0.05$).

desertification and/or shrub encroachment processes described elsewhere at landscape (van de Koppel *et al.*, 2002) and/or patch scales (Weber *et al.*, 1998). In these cases, the probability of biomass reduction or shrub encroachment will drastically increase when the distribution of herbivores is heterogeneous (Weber *et al.*, 1998; van de Koppel *et al.*, 2002). To document this effect analysis should focus on wider extents, distances, and grains than the ones used here.

Our study emphasizes the importance of taking into account the grain when analyzing spatial heterogeneity. In fact, it has been experimentally demonstrated that the grain of vegetation heterogeneity modifies significantly the selectivity and grazing habits of herbivores (Wallis DeVries, Laca & Demment, 1999). Our results were partially consistent with the general model suggesting that spatial heterogeneity decreases with grain (Wiens, 1989). Both the global and internal spatial heterogeneities decreased when grain increased (Figures 1 and 3a), but the spatial dependence did not change with grain, at least for grains ≤ 1 m (Figure 3b).

In conclusion, we have shown that, at least at these sites of the Patagonian steppe, a) the grazed sites are more heterogeneous than the 26-y-ungrazed site, b) spatial heterogeneity decreases with grain, c) the difference between grazed and ungrazed sites does not disappear as grain increases, and d) the spatial dependence does not change with grain or among differentially grazed sites. Further studies, with more replications per grazing treatment, are needed to test the regional validity of these locally valid conclusions.

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