

Ecosystem changes associated with grazing in subhumid South American grasslands

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Abstract

Question: What are the changes in vegetation structure, soil attributes and mesofauna associated with grazing in mesic grasslands?

Location: Southern Campos of the Río de la Plata grasslands, in south-central Uruguay.

Methods: We surveyed seven continuously grazed and ungrazed paired plots. Plant and litter cover were recorded on three 5-m interception lines placed parallel to the fence in each plot. We extracted soil fauna from a 10 cm deep composite sample and analysed the oribatids. Soil attributes included bulk density, water content, organic carbon (in particulate and mineral associated organic matter) and nitrogen content and root biomass at different depths. Changes in floristic, Plant Functional Types and mesofauna composition were analysed by Non-metric Multidimensional Scaling.

Results: Species number was lower in ungrazed than in grazed plots. Of 105 species in grazed plots only three were exotics. Shrub and litter cover were significantly higher inside the exclosures, while the cover of *Cyperaceae-Juncaceae* was lower. Grazing treatments differed significantly in plant and oribatid species composition. Grazing exclusion significantly reduced soil bulk density and increased soil water content. Carbon content in particulate organic matter was lower in the upper soil of ungrazed sites, but deeper in the profile, grazing exclosures had 8% more carbon in the mineral associated organic matter.

Conclusions: Our results generally agree with previous studies but deviate from the results of previous analyses in (1) the increase of shrub cover in ungrazed sites; (2) the redistribution of the soil organic carbon in the profile and (3) the low invasibility of the prairies regardless of grazing regime.

Keywords: Oribatide; Plant Functional Type; Soil attribute; Species richness; Uruguay.

Abbreviations: BMRPP = Blocked multi-response permutation procedures; INDVAL = Indicative values; MAOM = Mineral associated organic matter; NMDS = Non-metric multi dimensional scaling; POM = Particulate organic matter.

Nomenclature: Cabrera & Zardini (1978).

Introduction

The effects of grazing on the structure and functioning of grasslands, shrublands and savannas have generated controversy and debate in the literature (McNaughton 1979; Milchunas & Lauenroth 1993; Oesterheld et al. 1999; Chase et al. 2000). Grazing causes many community level changes. Prostrate growth forms tend to become more common at grazed sites in many grasslands (Facelli 1988; Díaz et al. 1992; Rodríguez et al. 2003). Shrub invasion of grasslands is considered a management problem in many parts of the world (Archer et al. 1988) but in other areas shrubs can decrease with grazing (Cipriotti & Aguiar 2004). Livestock may also affect the abundance and composition of soil fauna (Battigelli et al. 2003).

Grazing also influences the biogeochemical and physical properties of soils. The effects of grazing on soil organic matter contents are variable, showing both increases and reductions (Milchunas & Lauenroth 1993). Grazing also induces changes in root distribution and biomass, altering water and carbon dynamics (Milchunas et al. 1989; Milchunas & Lauenroth 1992). Trampling often reduces soil bulk density and soil water holding capacity (Taboada & Lavado 1988). In summary, grazing promotes changes at different hierarchical levels with multiple feedbacks (Brown & Allen 1989). In this article we focus on the integrated response of grasslands at community and ecosystem levels to domestic herbivore grazing.

The Río de la Plata grasslands are the most extensive biogeographic unit of the prairie biome in South America; they have been extensively modified by human activities (Guerschman et al. 2003). They occupy more than 700 000 km², distributed across eastern Argentina, Uruguay and southern Brazil (Soriano 1991). Steppes and prairies, though modified by grazing, still cover most of the area, mainly in the Uruguayan Campos and the flooding pampa

in Argentina (Soriano 1991). Experimental evidences from both the flooding pampa and the Uruguayan Campos showed that grazing increased species richness and modified the seasonal dynamics of carbon gains (Sala et al. 1986; Sala 1988; Rusch & Oesterheld 1997; Altesor et al. 1998; Chaneton et al. 2002; Rodríguez et al. 2003; Altesor et al. 2005). Studies of the impact of grazing on soil organic matter stocks were restricted to the upper soil layers and they did not discriminate among soil carbon pools with different turnover (Lavado et al. 1995; Chaneton & Lavado 1996). Thus, the changes in the more labile soil organic matter fraction may not have been detected because of their relatively small size compared to large passive pools.

Here we analyse the structural differences associated with grazing exclusion on vegetation, soil fauna and soil attributes at seven grazed-ungrazed paired sites. Our objectives were to evaluate the effect of grazing on the following attributes: plant and soil *Acari* species composition, plant and *Acari* richness, the relative abundance of Plant Functional Types (PFTs), vertical structure of the plant community, soil bulk density, root distribution, soil water content and soil organic carbon and nitrogen distribution. Apart from characterizing differences in these attributes in grazed and ungrazed plots, we evaluated predictions of two general hypotheses:

1. Grazing by domestic herbivores promotes species coexistence and it increases invasibility by reducing competitive exclusion, by increasing colonization through bare soil patches formation and by reducing litter cover. We predict that grazed areas would have: (a) a higher diversity and (b) a higher number and cover of exotic species.
2. Reduced carbon exports and herbivore respiration under grazing exclusion will increase carbon inputs to the soil and consequently soil organic carbon stocks, mainly in the labile soil organic matter fraction. We predict higher organic carbon contents in ungrazed plots and greater differences between grazing treatments for the more labile fraction.

Methods

The study site is located in the Southern Campos of the Río de la Plata grasslands, in south-central Uruguay (31°54' S, 58°15' W). The mean annual precipitation for the last 40 years was 1099 mm and the mean annual temperature for the same period was 17.4 °C, ranging from extremes of -0.7 °C in July to 39.6 °C in January (Anon. 2005). Total precipitation in 2002 was 1346 mm. In this area grazing usually leads to a two-tier system of vegetation: a low and dense stratum, no more than 5 cm high, and an upper stratum of bunch grasses

and small woody plants (Soriano 1991). C_4 native grasses dominated across the whole region, and mollisol is the main soil order (Paruelo et al. in press).

We established seven paired 1000-m² plots, grazed and ungrazed, at 'El Relincho', a 450-ha privately owned ranch. On the ranch cattle is raised on natural grasslands. Prior to the start of the experiment the area had been continuously grazed by cows at a moderate stocking rate (<0.5 animals/ha) for at least 25 years. In one of each paired plots domestic herbivores were excluded, while in the other grazing continued at the same stocking rates. Paired plots were less than 3 km apart and they were representative of the same grassland type ('mesophytic prairie', Perelman et al. 2001a; Lezama 2005). The mean age of exclosures was 7 a, ranging from 3 to 11 a. Previous analyses indicate that most of the vegetation changes took place during the early stages of the succession, particularly the two first years (Rodríguez et al. 2003). Soil data were collected from all the paired plots. Vegetation and mesofauna data were available for only six of the seven paired sites.

Field sampling

Plant and litter cover and canopy height were recorded in June 2002 on three 5-m interception lines placed parallel to the fence in each grazed and ungrazed plot. The transects were set < 4 m from each side of the fence, 1 m apart. Measurements were performed in the same soil patch. We recorded the projection of the portion of the canopy of each individual item intercepted by the line. We measured the height of plants and cover values were assigned to two height categories: low (< 10 cm) and upper (> 10 cm) strata. In addition to those intercepted by the lines we listed all species within the area defined by the first and third line surveyed (ca. 10 m²). The species were grouped into six PFTs: shrubs, summer grasses, winter grasses, *Cyperaceae-Juncaceae*, forbs and legumes.

We used one particular taxonomic group, the oribatids (*Acari*), to describe differences in soil mesofauna. In January 2003 we extracted six 5 cm diameter × 10 cm deep soil cores at each paired plot.

Bulk density and water content were sampled in June 2002 at 0-5, 5-10 and 10-30 cm by taking four 2-cm diameter soil cores. Ten additional soil cores were taken in each plot to make a pooled sample for C and N soil analysis. For sites with deep soils we also took three 5 cm diameter soil cores at 30-50, 50-70 and 70-100 cm depths. Roots were sampled at three depths (0-5, 5-10 and 10-30 cm) with a 5 cm diameter soil core, taking three replicates in the grazed sites and five replicates in the exclosures, because of the higher variation in roots spatial distribution in ungrazed conditions.

Laboratory analyses

Mesofauna samples were divided into two depths, 0-5 cm and 5-10 cm. We placed the samples in a modified MacFadyen extractor for soil fauna (MacFadyen 1962; Coleman et al. 1999). We determined species composition and abundance of each oribatid taxon.

Soil samples were placed in sealed bags and kept at 5 °C until processing. They were wet-sieved through a 2-mm sieve and large roots were manually removed. We then separated two different size fractions: the particulate organic matter (POM) of rapid turnover and the mineral associated organic matter (MAOM) of low turnover (Cambardella & Elliot 1994). Carbon and nitrogen content were analysed for each soil fraction with a Carlo Erba Elemental Analyzer at the Duke Environmental Stable Isotope Laboratory.

For deep samples (> 30 cm) the POM C and N were not estimated because the low C-content generated errors in the automated element analyzer. In these samples carbonates were extracted using a weak acid (HCl 0.5N), prior to the determination of organic C and N. Roots were washed and separated from soil using a 2-mm sieve. Roots were oven-dried at 60-70 °C and weighed.

Data analyses

Differences in mean plant species richness, PFTs and litter cover between grazed and ungrazed plots were tested with paired *t*-tests. Differences in floristic, PFT and mesofauna composition were analysed by Non-metric Multidimensional Scaling (NMDS) with Bray-Curtis distances. The analyses were performed with PC-Ord (McCune & Mefford 1999). The floristic matrix contained 12 plots and 150 species and the PFTs matrix included 12 plots and six functional groups. The mesofauna results from the two strata were added, so the *Acari* matrix was conformed by 12 plots and 39 species.

The proportion of variance accounted for by each axis was estimated by Pearson's r^2 . We tested multivariate differences among plots in plant and *Acari* species composition and PFTs using Blocked Multi-Response Permutation Procedures. We used the INDVAL (Indicative Values) procedure to identify plant and *Acari* indicator species of ungrazed vs. grazed plots (Dufrêne & Legendre 1997).

Differences in soil bulk density, water content and root biomass between grazed and ungrazed treatments were compared with paired *t*-tests for depths 0-5, 5-10 and 10-30 cm. For POM differences in mean soil organic C and N were calculated for these depths, while for the MAOM comparisons were performed for the 30-50, 50-70 and 70-100 cm layers. Mean values for each depth were compared by paired *t*-tests.

Results

Overall, we recorded 70 plant species in the exclosures and 105 species in the grazed plots. A small fraction included three exotic species (4.2%) in the ungrazed and four (3.8%) in the grazed plots. Species richness S was significantly lower in ungrazed ($S_U = 37.1 \pm 3.43$) than in grazed plots ($S_G = 53.14 \pm 4.07$, mean \pm SE) ($t = 5.04$, $df = 5$, $P = 0.004$).

The vertical structure of vegetation differed between grazing treatments. In the lower stratum (< 10 cm) plant cover was 75.7% and 13.7% in grazed and ungrazed plots, respectively ($t = -5.59$, $df = 5$, $P = 0.002$). In contrast, the cover of the upper stratum was higher in the exclosures (75% vs 25.1%) ($t = 10.17$, $df = 5$, $P = 0.0001$). Inside the exclosures litter cover was also significantly higher than in grazed sites, 8.9% and 3.1%, respectively ($t = 3.39$, $df = 5$, $P = 0.02$). Shrub cover was significantly higher inside the exclosures while the cover of *Cyperaceae-Juncaceae* was lower than in grazed plots (Fig. 1). The cover of forbs, summer and winter grasses (Fig. 1) and bare soil did not differ significantly between grazing regimes. In four out of six exclosures winter grasses showed a higher cover in the exclosures (Fig. 3).

Grazing significantly altered species composition (Blocked Multi-Response Permutation Procedures (BMRPP): $d = 27.45$, $P = 0.0098$) (Biondini et al. 1985). The ordination of the floristic matrix showed a clear discrimination between ungrazed and grazed plots in the axes that explained most of the variance ($r^2 = 0.69$, $r^2 = 0.19$, for axis 1 and 2, respectively; Fig. 2a). All grazed plots had a higher cover of prostrate, warm-season species

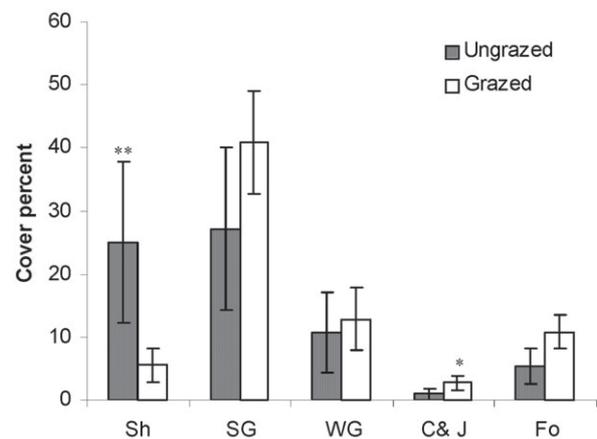


Fig. 1. Mean PFT cover (%) of grazed and ungrazed plots. Sh = Shrubs; SG = Summer grasses; WG = Winter grasses; C&J = *Cyperaceae* and *Juncaceae* and Fo = forbs. Bars represent standard error. Statistical differences ($P < 0.05$, $P < 0.01$) (paired *t*-test) between grazed and ungrazed plots are indicated by * and **, respectively.

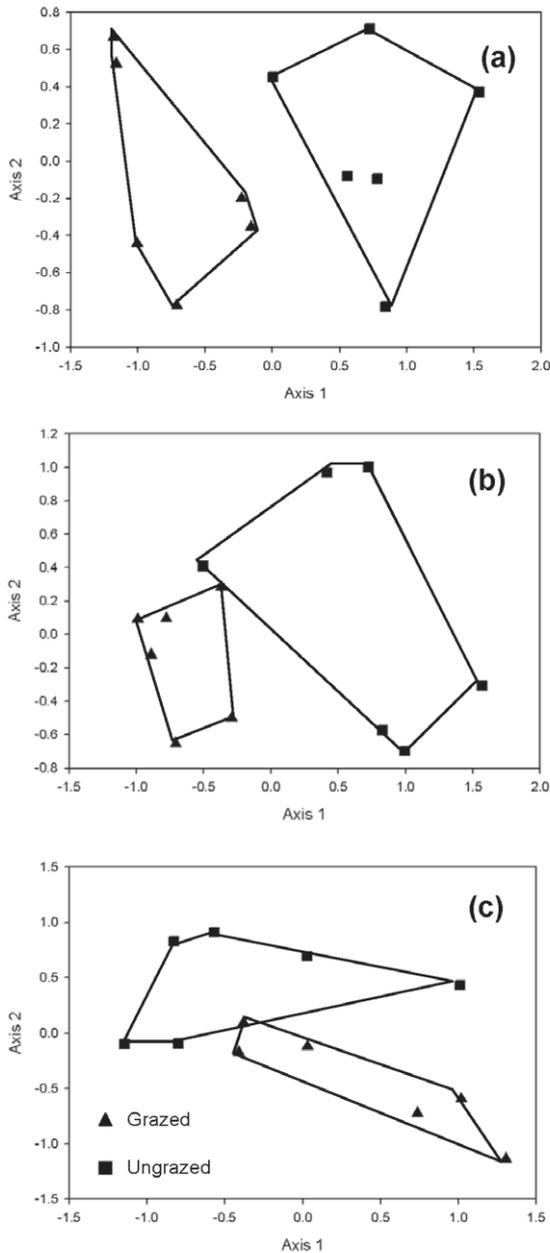


Fig. 2. Configuration of grazed (▲) and ungrazed (■) plots of (a) the floristic cover matrix, (b) PFTs and (c) *Acari* abundance in a two-dimensional Non-Metric Multidimensional Scaling (NMDS) representation of the Bray-Curtis distances.

such as *Paspalum notatum*, *Axonopus affinis* and *Stenotaphrum secundatum*. In most of the ungrazed plots shrubs were more abundant, particularly *Eupatorium buniifolium*. The dominant grass in ungrazed plots varied among plots, but included *Stipa neesiana*, *S. charruana*, *Coelorachis selleana* and *Cynodon dactylon*. *Paspalum quadrifarium*, a tall summer grass, was the dominant species in just one of the exclosures.

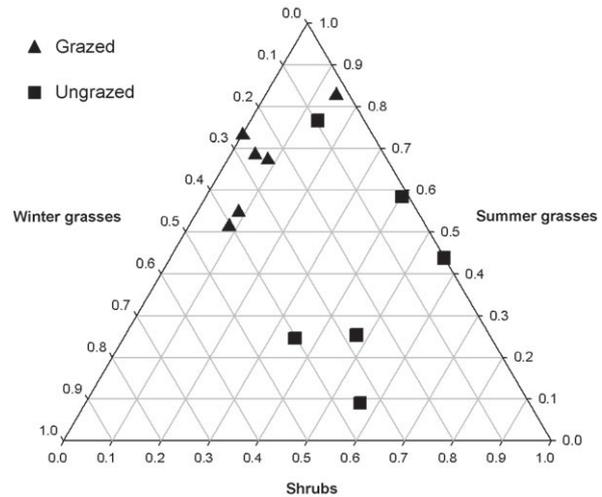


Fig. 3. Triangular ordination of grassland plots with different grazing regimes grazed (▲), ungrazed (■), according to the upper layer cover of shrubs, summer and winter grasses. Values correspond to total plant cover (%) mean values per plot ($n = 6$).

According to the INDVAL analysis, the influence of grazing was indicated by four forbs: *Chevreulia sarmentosa*, *Dichondra sericea*, *Gamochaeta* spp. and *Eryngium nudicaule*, and three C_4 grasses: *Axonopus affinis*, *Paspalum notatum* and *Aristida* spp. The forbs were rosettes, two of the grasses were prostrate and one was a short grass (*Aristida* spp.). The ungrazed condition featured three shrub species: *Eupatorium buniifolium*, *Baccharis articulata* and *B. trimera*, three C_3 grasses (*Stipa neesiana*, *S. papposa*, *Briza subaristata*) and a C_4 grass (*Schizachyrium microstachyum*).

The cover of the species corresponding to the different PFTs also differed significantly according to grazing conditions (BMRPP: $d = 0.29$, $P = 0.008$). The ordination (Fig. 2b) clearly separated ungrazed and grazed plots ($r^2 = 0.82$ and $r^2 = 0.14$, for axes 1 and 2, respectively), primarily in the shrub dimension. Five out of six ungrazed plots had a shrub cover $> 35\%$ (Fig. 3), with five grazed plots having shrub cover $< 10\%$. Both grazing regimes showed the same range of cover by winter grasses (0-40%; Fig. 3). Structural heterogeneity, defined from PFTs proportions, was higher in ungrazed than in grazed plots.

For the soil fauna data, we recorded 37 morphospecies and three families: *Shelorbitidae*, *Oppidae* and *Galumnidae*. *Acari* richness was higher in ungrazed plots only in the first 0-5 cm depth ($S_U = 16.3$, $S_G = 11.8$, $P = 0.07$). Species composition also differed between ungrazed and grazed plots (BMRPP: $d = 5.29$, $P = 0.02$). As for plant attributes, the ordination separated plots according to the grazing regimes ($r^2 = 0.49$, $r^2 = 0.36$, for axes 1 and 2, respectively) (Fig. 2c). Two *Acari*

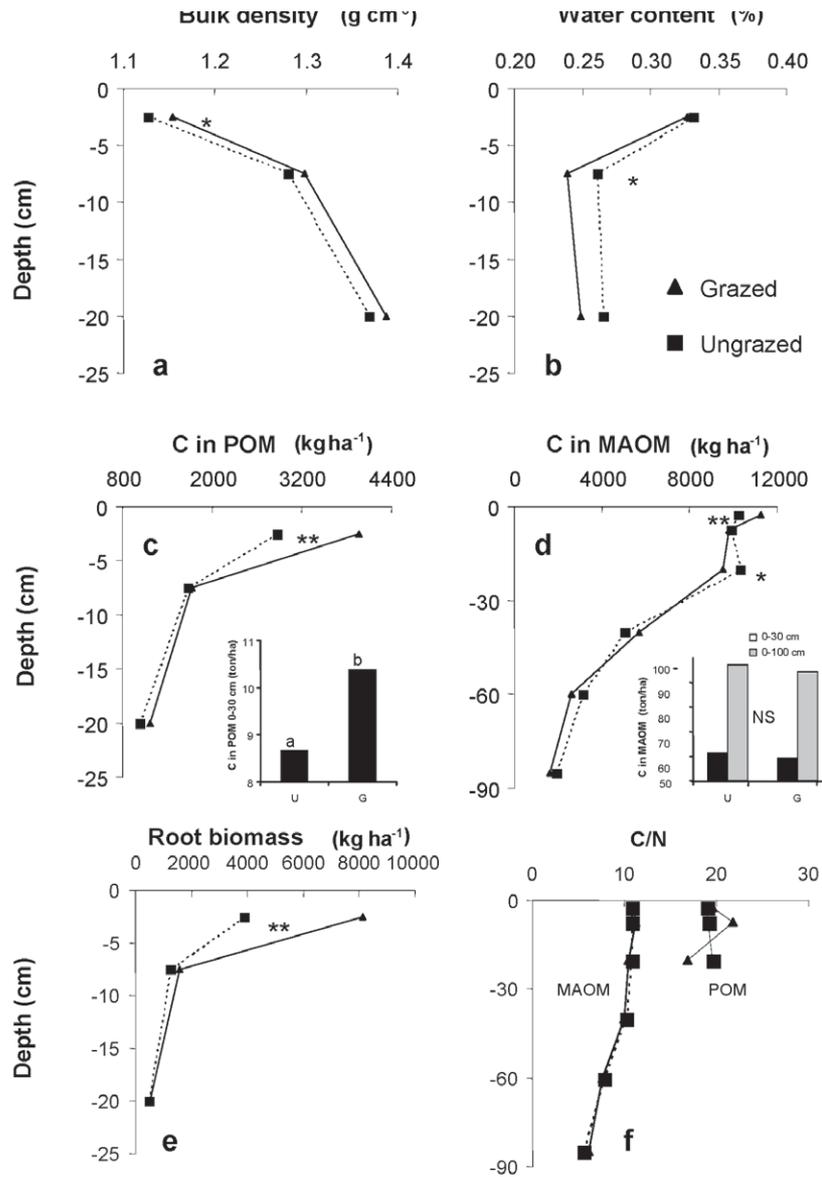


Fig. 4. Soil depth profile of : (a) bulk density (g/cm²) sampled at 0-5, 5-10 and 10-30 cm; (b) water content (%); (c) C in the POM (kg ha⁻¹); (d) C in MAOM (30-50, 50-70 and 70-100 cm); (e) Root biomass (kg ha⁻¹); (f) C:N ratio of the POM and MAOM fraction. Inset in (c) and (d) shows mean total C in POM fraction for 0-30 cm depth and total mean of C in MAOM fraction for 0-30 and 0-100 cm depth, in grazed (G) and ungrazed (U) plots. Values are a mean across the seven paired sites; ▲ = grazed ■ = ungrazed. Statistical differences (*t*-test) between grazed and ungrazed soil for each depth are indicated as * = *p* < 0.1 and ** = *p* < 0.05.

species were associated with grazing: *Tectocephus depressus* and *Hemileius suramericanus*. The family *Oppidae* had large and significant INDVAL values associated with ungrazed conditions.

Soil bulk density did not significantly differ between grazed and ungrazed plots ($t = -2.15$, $df = 6$, $P = 0.07$; Fig. 4a). Soil water content (measured in mid-winter) was almost 10% higher at 5-10 cm in ungrazed sites ($t = 2.357$, $df = 6$, $P = 0.05$) but did not differ significantly between upper and lower layers (Fig. 4b). Carbon in POM was not significantly different in the first 30 cm of

the profile ($t = -1.923$, $df = 6$, $P = 0.10$; Fig. 4c, inset). Differences were mainly due to changes in the 0-5 cm layer where C in POM was 28% higher in grazed sites ($t = 2.645$, $df = 6$, $P = 0.04$) (Fig. 4c). A similar trend was observed for the C in the MAOM fraction, since grazed sites had 9.0% more carbon at 0-5 cm (Fig. 4d; $t = -3.28$, $P = 0.017$). The MAOM fraction did not significantly differ between grazed and ungrazed plots ($t = 2.290$, $df = 6$, $P = 0.062$). For the 0-30 cm layer, C in MAOM was 3.6% higher in ungrazed sites but the differences were not significant (Fig. 4d, inset), this was also the case for

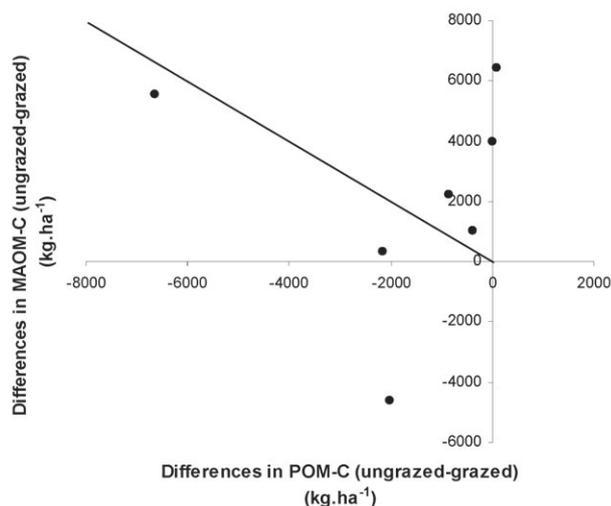


Fig. 5. Relationship between carbon differences in the POM and MAOM, for 0–30 cm of seven paired grazed and ungrazed sites. Negative values represent losses of carbon at the ungrazed sites. The solid line represents the situations where decreases in POM-C are compensated by the increases of MAOM-C (no changes in total C).

C content in the 30–100 cm layer (Fig. 4d, inset).

As shown in Fig. 4c (inset) all the ungrazed plots presented lower C contents in the POM fractions. Net C accumulation in the soil profile in the exclosures depends on the magnitude of changes in the MAOM carbon. A plot of the changes in POM and MAOM carbon for the individual sites (Fig. 5) shows that in four out of seven sites the changes in MAOM carbon compensate the reduction in POM. At only one plot carbon contents was lower in both POM and MAOM fractions in the exclosures (Fig. 5).

Grazed sites had almost twice as much root biomass in the top 5 cm of soil, (Fig. 4e) ($t = -2.653$, $df = 6$, $P = 0.04$). No differences in root biomass were observed at 5–10 or 10–30 cm. The C:N ratio of the POM fraction was higher under grazing in the first 10 cm of soil and lower for the 10–30 soil depth, but differences were significant only at 5–10 cm (Fig. 4f). Although marginally significant, this vertical pattern in C:N ratios suggest that residues are more recalcitrant under grazing only in surface layers (note that the same vertical pattern is reproduced by the MAOM fraction). As expected, the C:N ratio of the MAOM fraction was lower than the POM fraction and decreased with depth (Fig. 4f), but no significant differences were observed between grazing regimes. As a result of the changes in both C:N and the size of the pools, the increases in MAOM compensate for N losses due to POM decreases in most of the plots (Fig. 5).

Discussion

As many other studies have shown (Leetham & Milchunas 1985; Collins et al. 1998; Milchunas et al. 1998), our results suggest a strong influence of grazing on vegetation structure, soil fauna and soil attributes. However, the magnitude and direction of some of the changes associated with grazing differed from previous studies in temperate subhumid grasslands. Three results were particularly interesting: the increase of shrub cover in ungrazed sites, the low invasibility of the prairies regardless of the grazing regime and the redistribution of organic carbon in the soil profile.

Plant community

The absence of grazing in the Uruguayan Campos promoted shrub increase. Many studies in mesic grasslands have shown the opposite (Bragg & Hulbert 1976; McPherson et al. 1988; Roques et al. 2001; Briggs et al. 2005; Lett & Knapp 2005). In the present study, the effect of grazing is not mediated by fire as suggested by these authors. Río de la Plata grasslands grow in a less seasonal environment than northern hemisphere grasslands (Paruelo et al. 1995). This does not allow the accumulation of large quantities of standing dead material. In fact, during winter the amount of green biomass is higher in the Río de la Plata grasslands than in similar sites of North America and prevents regular burning (Altesor et al. 2005; Guerschman & Paruelo 2005).

The increase of woody plant abundance in most temperate humid grasslands is due to the expansion of forests or isolated trees that generate a savanna-like physiognomy (Ghersa et al. 2002). In the present study, the woody components most represented in ungrazed sites are four nanophanerophytes ca. 0.5–2 m tall (*Eupatorium buniifolium*, *Baccharis spicata*, *B. articulata*, *B. dracunculifolia*) and two chamaephytes (*Baccharis trimera* and *B. coridifolia*) that grow to ca. 0.5 m (Cabrera & Zardini 1978). The shrub richness in grazing exclosures increased from six to ten species.

Why do shrubs become abundant in exclosures? In the absence of disturbance (fire, grazing or mowing) shrubs are able to establish and grow taller than the grasses, culminating in higher woody densities as shown in other mesic grasslands (Van Dyke et al. 2004) or in wetlands (Nunes da Cunha & Junk 2004). The sensitivity of seedlings and new sprouts to occasional grazing would reduce shrub biomass and increase their mortality. Additionally, the changes in the light environment generated by the accumulation of dead material under ungrazed conditions may be advantageous to a PFT able to better distribute the leaf area in the vertical dimension.

Another important difference from previous studies

is the lack of grazing impact on the number of exotic species. Only one more exotic species was recorded in grazed plots than in the exclosures. The absence was not related to the lack of propagules. Preliminary analyses of the seed bank (Haretche & Rodriguez 2004) revealed viable seeds of many exotic species in the prairie soil seed bank. Most of these species are weeds in nearby crops and pastures. Exotic species, mainly cool season dicotyledons, become an important component of the community in the flooded pampa (Facelli 1988; Rusch & Oesterheld 1997), another subregion of the Río de la Plata grasslands. Perelman et al. (2001b) found, for the Argentine pampa, a negative relationship between the richness of exotic species and the relative importance of C_4 grasses. Our data, corresponding to an area not included in the Perelman et al. (2001b) analysis, showed an even higher C_4 grass importance than the extreme sites considered in their study, thus providing additional support to this relationship. The grazing regime (the presence or absence of domestic herbivores) and the availability of propagules do not seem to substantially modify the invasibility of the prairies of the Uruguayan Campos. Less than 4% of the flora is exotic regardless of the grazing regime.

Our results, which highlight the positive effect of grazing on plant diversity, agree with previous studies both in this region and in grasslands worldwide (Trémont 1994; Rusch & Oesterheld 1997; Olf & Ritchie 1998).

Mesofauna

Grazing had a significant effect on the saprophytic community. Grazing exclusion altered the composition, size and richness of important soil taxa (i.e. *Acari*). The genera *Hemileius* and *Tectocephus* that indicate grazed conditions are cosmopolitan. The genera more represented in ungrazed plots belong to the *Oppidae* (*Oxyoppia pilosa* and *Brachyoppia deliciosa*) and *Suctobelbidae*. *Oppidae* are fungivorous and *Suctobelbidae* are probably liquid feeders (Behan-Pelletier 1997). All of them are common in disturbed or agricultural sites (Lagerlöf & André 1988; Behan-Pelletier 1999). The higher richness of *Acari* in ungrazed plots might be related to litter accumulation. Our results partially support the hypothesis that grazing promotes species coexistence by reducing competitive exclusion and by increasing colonization through bare soil patches formation and reducing litter cover. As predicted from such hypothesis, both *Acari* and plant species richness increased under grazed conditions. However, invasibility did not increase. Exotic species abundance, as discussed above, was low regardless the grazing treatment.

Soil characteristics

Although we did not detect changes in total soil C among grazing treatments, we observed a differential effect on the labile and recalcitrant fraction of the soil organic matter (Figs. 4c,d and 5). Soil carbon was higher under grazing in the 0-5 cm layer, probably due to the higher biomass of below-ground organs. The pattern changed for deeper layers (10-30 cm): C stocks at this depth were higher in ungrazed sites due to an increase in the more recalcitrant organic matter pool.

Shrub encroachment has been identified as a major factor responsible for the increase of total C (Pacala & Hurr 1993; Briggs et al. 2005). Such changes should be related to the amount of structural tissues produced by woody species. Increases in shrub abundance could be responsible for the increases in C in deep layers in ungrazed conditions. Shrubs, generally, have relatively deeper roots than grasses (Sala et al. 1994; Jackson et al. 2002; Schenk & Jackson 2002).

Grazing increases N-volatilization from urine and dung patches (Frank & Zhang 1997; Whitehead & Raistrick 1993). In the exclosures such N-outputs would not occur, leading to increases in N-pools. However, N accumulation was not evident throughout the whole profile but only in layers deeper than 10 cm. The higher N losses in grazed plots may be partially compensated for by the higher N-inputs associated with the high root biomass of the upper soil layer under grazing. N accumulation in the ungrazed plots would promote increases in soil C (Pineiro et al. 2002).

Our results did not support our initial hypothesis on the effect of grazing on soil organic carbon levels: the reduction in C exports and herbivore respiration under grazing exclusion would increase soil organic C stocks, mainly in the labile soil organic C fraction. At least in the short term, the dynamics of soil organic C seems to be influenced in a complex way by changes in C inputs and vertical distribution, in N-availability and in PFT composition. The differential response of the labile and recalcitrant organic matter fraction to grazing exclusion highlight the importance of tracking both pools separately and the need for long-term analyses. Short-term studies would probably allow us to perceive only differences in POM. Our results showed an increase of the labile fraction in the upper soil under grazing. The older exclosures analysed (>10 a) presented an important increase in the low turnover fraction (MAOM) that compensate for the superficial increase in POM (Fig. 5).

Our study highlighted some important issues regarding the impact of grazing: the increase of shrub cover in ungrazed sites, the redistribution of the soil organic carbon in the profile and the low invasibility of

the prairies regardless of grazing regime. It also raises new questions: Given the different behaviour of subregions of the Río de la Plata grasslands that share the same potential flora (Campos and the flooding pampa), is the environment (flooding regime, magnitude of water stress) controlling the success of exotic species in the native prairies? Is the observed shrub increase a transient response that will revert in the long-term? Which of the environmental changes induced by grazing exclusion promote the increase of shrub cover? How did the changes in PFT composition and N-cycling mediated by grazing affect the availability of C-sequestration of grasslands?

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