Effect of grazing on community structure and productivity of a Uruguayan grassland

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Abstract

Grasslands and their grazers provide some of the most compelling examples for studying the relationship between diversity, productivity, and disturbance. In this study, we analyzed the impact of grazing-induced changes in species composition and community structure upon the productivity of a grassland in the Campos region, Uruguay. We compared three treatments: a continuously grazed area, a 9-year old exclosure to domestic herbivores, and grazing-simulated plots inside the exclosure, which were clipped so that their standing biomass resembled that of the grazed area. We studied the community composition of the grazed and ungrazed situations, and determined biomass and above-ground net primary production (ANPP) of the three treatments during 1 year. Grazed plots had higher species richness and diversity than the exclosure. Grazing resulted in the replacement of some cool-season, tussock grasses by warm-season, prostrate grasses. ANPP was 51% higher under grazing than in the exclosure, but the grazing-simulated plots inside the exclosure were the most productive treatment, 29% higher than the grazed plots. Thus, two components of grazing effect may be postulated for this grassland. The structural component resulted in higher ANPP, probably due to the elimination of standing dead biomass. The species composition component resulted in lower ANPP once the structural component was controlled, probably due to the shift to warm-season phenology and prostrate habit. Our findings contrast with a similar experiment carried out in the neighbouring Flooding Pampa region, which suggests that the relationship between grazing and community structure and function is difficult to generalize.

Introduction

Grazing is a key disturbance that shapes the structure and function of grassland communities (McNaughton 1983a, 1985). Structurally, grazing modifies the species composition, richness, vertical profiles, plant traits, and a number of other attributes of grasslands (Noy-Meir et al. 1989; McIntyre and Lavorel 2001; Rodríguez et al. 2003). Functionally, grazing alters the flow of energy and the cycling of materials, both directly, through defoliation, trampling, and dung and urine depositions, and indirectly, through modification of species composition and species interactions (Schlesinger et al. 1990; Aguiar et al. 1996; Hobbs et al. 1996).

The relationships between a structural trait, species diversity, and a functional trait, primary productivity, is at the core of a current debate within the more general, but also current

discussion on the relationship between biodiversity and ecosystem function (e.g., Naeem and Wright 2003). As stated above, grasslands and their grazers provide one of the strongest and widespread cases for studying the relationship among diversity, productivity, and disturbance. Grazing drastically alters plant species composition, particularly in mesic grasslands, and it also affects above-ground net primary production (ANPP, Milchunas and Lauenroth 1993; Oesterheld et al. 1999).

How do the grazing-induced changes in species composition and diversity translate into changes of ANPP? This is a difficult question to answer because of the problems faced when trying to isolate the effects of grazing on ANPP that stem from changes in species composition and diversity from those that stem from changes in other ecosystem attributes affected by grazing. Rusch and Oesterheld (1997) attempted to isolate these two sets of effects in the Flooding Pampa grasslands of Argentina. There, grazing reduced ANPP by a factor close to 7 compared to ungrazed, long-term exclosures, but it increased mean species richness from about 15 to 25 species. Most of this increase was accounted for by exotic forbs, which have a cool-season phenology. In contrast, the native grasses abundant in the exclosures were mostly warm-season growers. In order to isolate the effect of grazing on species richness from that on plant biomass, they studied the ANPP of exclosure plots from which biomass had been mechanically removed to leave an amount of leaf biomass resembling the grazed condition. ANPP in these plots was still higher than in the grazed areas, which lead the authors to conclude that the shift in species composition and diversity was highly responsible for the reduction of ANPP caused by grazing.

The Flooding Pampa in Argentina and the Campos in Uruguay and southern Brazil comprise one of the largest areas of natural temperate sub-humid grasslands in the world, covering an arc folded around the Rio de la Plata (Soriano 1991). Large areas have been replaced by crops, but an important portion of the region is still occupied by natural or semi-natural grasslands grazed by domestic herbivores, mainly cattle and sheep (Soriano 1991; Altesor et al. 1998). In Uruguay, the area occupied by natural grasslands amounts to more than 140,000 km^2 (ca. 87% of the country). Artificial prairies cover only 3% of the area.

The effect of grazing on species composition in the Campos of Uruguay is different from the patterns observed in the Flooding Pampa. As in the Flooding Pampa, grazing increases species richness, but instead of promoting cool-season exotic forbs, it results in the dominance of prostrate grasses, which spread by means of rhizomes and stolons, and non-palatable native forbs. Another important difference is that within the native grasses, there is a shift from cool-season growers inside the exclosures to warm-season growers outside (Altesor et al. 1998; Rodríguez et al. 2003).

In this study, we analyzed the impact of grazing-induced changes in species composition and community structure upon productivity of the Campos grasslands of Uruguay. Using a similar approach to that of Rusch and Oesterheld (1997), we evaluate current theories addressing the relationship between species diversity and productivity when these factors are under the influence of grazing. Our main objectives were (1) to compare the species and plant functional type composition of grazed and ungrazed sites, (2) to assess the effect of grazing-induced changes in species composition upon ANPP, and (3) to assess the effect of grazing-induced changes in canopy structure upon ANPP.

Methods

Study site and treatments

The study site belongs to the Southern Campos of the Rio de la Plata grasslands. It is located in Ecilda Paullier, *Departamento de San José*, in south-central Uruguay (34°19′ S, 57°02′ W). The average annual precipitation of the last 40 years was 1370 mm, and the mean temperature for the same period was 18.9 °C, ranging from 12.6 °C in July to 26.3 °C in January. In this area, grazing usually leads to a two-strata system: a low and dense stratum, no more than 5 cm high, and a higher stratum of bunch grasses and small woody plants (Soriano 1991). C_4 native grasses dominate across the whole subregion.

We performed our study in two contiguous areas, grazed and ungrazed, 1000 m^2 each, at the *El Relincho* ranch, within a 500 ha grazed paddock. The site is situated on a homogeneous mollisol, a typical prairie soil. We compared three treatments: (1) a grazed area (G), which had been

continuously grazed for at least 25 years at a moderate stocking rate (<0.5 animals/ha), (2) an ungrazed area (U), which had been excluded from domestic herbivores for 9 years, and (3) grazing-simulated plots (GS) inside the exclosure, where we clipped the vegetation to standardize the standing biomass between G and U. The design is pseudoreplicated for the grazed–ungrazed contrasts. However, the exclosure was located in a way that plant community structure inside and outside the exclosure was similar at the beginning of the exclusion period. Thus, we believe that the grazing treatment is the major cause for the eventual differences inside vs. outside the exclosure.

Species composition

Species composition of the G and U treatment was surveyed in December 2000. Frequency values were estimated by recording all the species contacts made by a needle (0.4 mm diameter) vertically lowered through the canopy (Tothill 1978). In each treatment, a total of 100 observations were distributed every one meter along two 50-m transects. Based on these frequency estimates, we calculated species richness (S), Shannon's diversity index (H), and evenness (E).

Above-ground net primary production

ANPP was estimated on the basis of above-ground biomass harvests sequentially performed in March, June, September and December 2000, and March 2001 in the three treatments. In G, biomass was determined inside three 5×5 m moveable cages (replicates), which were randomly located every harvest day. Inside each cage, we harvested three randomly selected 70×70 cm quadrats (3 subsamples/replicate). Every harvest day, except for March 2000 and 2001, two sets of harvests were performed, one before moving the cages, to estimate the biomass produced during the period ending that date, and another one after moving the cages, to estimate the initial biomass for the subsequent period. In March 2000 and 2001, only one set of biomass harvests was performed, the initial set for the period March–June, and the final set for

the period December 2000–March 2001. Fresh weight was recorded *in situ* and used to set the amount of biomass to be removed from GS plots (see below). In U, above-ground biomass was harvested each date from nine 70×70 cm quadrats. In GS, biomass was also harvested from nine 70×70 cm quadrats, but these quadrats had been clipped at the start of each season to the height that left a remaining biomass equivalent, in fresh weight, to the average initial biomass harvested in G. Sampling within the exclosure (U and GS) was random, but stratified to avoid patches with dense shrub cover (there were no such patches in G). At both treatments, the quadrats were grouped in sets of three, as in G.

The harvested material was sorted in the field into cool-season and warm-season species. In the laboratory, each group was separated into green and standing dead biomass. Afterwards, biomass was dried at 70 °C and weighed to constant weight. ANPP was estimated for the period between harvests following Sala et al. (1981) and considering the functional types, cool-season and warm-season species, separately. Thus, ANPP of each functional type resulted from: ANPP = G + Sc, where G was the positive difference of two successive measurements of the green biomass compartment divided by the number of days between harvests. When the difference was negative the value calculated was called net senescence (S). Sc represented the increment of standing dead material divided by the number of days between harvests minus the net senescence and it had the restriction of being ≥0. Total ANPP resulted from the sum of the ANPP of each functional type.

Differences in biomass and productivity among treatments at each season were analyzed using ANOVAs, coupled with Tukey's multiple *t* tests for comparison of means when main effects were significant.

Results

Species composition and diversity

Species richness, diversity, and evenness were higher in the grazed area than in the exclosure. Life-form community composition also differed between sites (Table 1).

Table 1. Shannon's diversity index (H'), species richness (S), evenness (E), and percentage of graminoids (grasses, sedges and rushes), forbs, and shrubs under grazed (G) and ungrazed (U) regimes (mean $\pm$ 1 SD).

	G	U
H'	3.59 $\pm$ 0.16	3.03 $\pm$ 0.05
S	50 $\pm$ 5.66	34.5 $\pm$ 2.12
E	0.918 $\pm$ 0.013	0.856 $\pm$ 0.001
Graminoids (%)	60.06 $\pm$ 1.14	64.01 $\pm$ 8.03
Forbs (%)	33.90 $\pm$ 1.82	22.98 $\pm$ 6.78
Shrubs (%)	6.04 $\pm$ 0.68	13.01 $\pm$ 1.25

Mean frequency values of warm-season species represented 53 and 41% under grazing and exclosure respectively. The dominant group under grazing regime included C_4 prostrate grasses like *Paspalum notatum*, *Stenotaphrum secundatum*, *Cynodon dactylon*, and one C_3 erect grass: *Stipa neesiana*. Only four alien species were recorded in this area. Most of the dominant species were replaced in the exclosure by C_3 erect grasses (*Stipa papposa*, *Piptochaetium bicolor*, *Danthonia cirrata*) and *Eupatorium buniifolium*, a shrub species. No alien species were recorded in the exclosure (Table 2).

Above-ground net primary production (ANPP)

Productivity was maximum in the treatment that simulated grazing inside the exclosure, intermediate under grazing, and minimum in the ungrazed treatment (Figure 1). ANPP in G was 51.3% higher than in U (Figure 1, $ANPP_G = 602$ g m^{-2} year^{-1} and $ANPP_U = 398$ g m^{-2} year^{-1}). The ANPP in GS ($ANPP_{GS} = 777$ g m^{-2} year^{-1}) was 29% higher than in G.

Cool-season species accounted for a larger proportion of productivity than warm-season species in U and GS, whereas warm-season species accounted for most of the productivity in G (Figure 1). Warm-season species productivity peaked in spring and summer, and was significantly higher in G than in the other treatments (spring $F_{2,6} = 17.5$, $p = 0.003$, summer $F_{2,6} = 22.5$, $p = 0.002$). Cool-season species productivity was significantly greater in GS than in the other treatments in autumn and spring (autumn $F_{2,6} = 7.7$, $p = 0.022$, spring $F_{2,6} = 35.3$, $p = 0.0001$).

In autumn and spring, the amount of green biomass did not differ significantly among treatments. In winter, it was significantly greater in U than in G and GS ($F_{2,6} = 8.1$, $p = 0.019$). In summer, G had more green biomass than GS ($F_{2,6} = 6.3$, $p = 0.034$). At most seasons, standing dead biomass was higher in U and GS than in G (autumn $F_{2,6} = 42.6$, $p = 0.0001$, winter $F_{2,6} = 61.8$, $p = 0.0001$, spring $F_{2,6} = 5.1$, $p = 0.05$), except in summer when the treatments did not exhibit significant differences (Figure 2).

Discussion

Compared to the exclosure, grazing drastically increased diversity, both in terms of number of species and evenness. These findings confirm previous reports for other grasslands in Uruguay (Rodríguez et al. 2003), the Flooding Pampa (Rusch and Oesterheld 1997), and world wide (Milchunas and Lauenroth 1993). There was also a shift of dominant species between the grazed and ungrazed treatments. Grazing-induced changes mainly consisted of prostrate warm-season species such as *Paspalum notatum* and *Stenotaphrum secundatum*, replacing erect cool-season species like *Stipa papposa*, *Piptochaetium bicolor*, and *Danthonia cirrata*. These functional changes within dominant grasses have been observed in other grasslands of Uruguay (Rodríguez et al. 2003). Our results also showed an increase in the number of forbs in the grazed area. There were 22 species of forbs exclusive to the grazed community, and 64% of them were warm-season species. Only one exotic forb was registered (*Hipochoeris radicata*). In contrast, in the Flooding Pampa grasslands, grazing promoted the addition of exotic cool-season species, which displaced the warm-season grasses from higher dominance ranks towards subordinate rank position (Rusch and Oesterheld 1997).

The higher ANPP registered in the grazed treatment (G) compared to the ungrazed area (U) contrasts with the response observed in the Flooding Pampa, where the grazed situation was much less productive than the ungrazed one (Rusch and Oesterheld 1997). These authors suggested that the identity of the dominant species (rather than the number *per se*) could account for the differences observed. The decline of ANPP in

Table 2. Mean frequency of graminoids (grasses, sedges and rushes), forbs, and shrubs present in grazed (G) and ungrazed (U) areas.

Species	Family	Origin	F.G.	Mean frequency	
				G	U
Graminoids					
Stipa neesiana	Poaceae	N	c-s	9	10
Carex phalaroides	Cyperaceae	N	c-s	5	0.5
Stipa charruana	Poaceae	N	c-s	5	0.5
Piptochaetium bicolor	Poaceae	N	c-s	4	13.5
Piptochaetium montevidense	Poaceae	N	c-s	3.5	1
Stipa megapotamia	Poaceae	N	c-s	2.5	8.5
Briza subaristata	Poaceae	N	c-s	2	7.5
Stipa papposa	Poaceae	N	c-s	2	18
Melica brasiliana	Poaceae	N	c-s	1.5	1.5
Danthonia cirrata	Poaceae	N	c-s	0.5	10
Stipa trichotoma	Poaceae	N	c-s	0.5	0.5
Bothriochloa laguroides	Poaceae	N	w-s	4.5	0.5
Coelorhachis selloana	Poaceae	N	w-s	5	3
Juncus sp.	Juncaceae	N	w-s	3	1.5
Panicum sabulorum	Poaceae	N	w-s	2.5	1
Cyperus sp.	Cyperaceae	N	w-s	2	1
Paspalum plicatulum	Poaceae	N	w-s	2	4.5
Paspalum quadrifarium	Poaceae	N	w-s	2	1
Setaria vaginata	Poaceae	N	w-s	2	2
Andropogon ternatus	Poaceae	N	w-s	1	2.5
Panicum hians	Poaceae	N	w-s	0.5	1.5
Sporobolus indicus	Poaceae	N	w-s	0.5	0.5
Sporobolus platensis	Poaceae	N	w-s	0.5	1
Briza minor	Poaceae	E	c-s	2	
Piptochaetium stipoides	Poaceae	N	c-s	1.5	
Calotheca brizoides	Poaceae	N	c-s	1	
Phalaris platensis	Poaceae	N	c-s	1	
Bromus catharticus	Poaceae	N	c-s	0.5	
Lolium multiflorum	Poaceae	E	c-s	0.5	
Piptochaetium lasianthum	Poaceae	N	c-s	0.5	
Vulpia australis	Poaceae	N	c-s	0.5	
Paspalum notatum	Poaceae	N	w-s	10.5	
Cynodon dactylon	Poaceae	E	w-s	6.5	
Stenotaphrum secundatum	Poaceae	N	w-s	6	
Paspalum dilatatum	Poaceae	N	w-s	3	
Axonopus affinis	Poaceae	N	w-s	2.5	
Aristida venustula	Poaceae	N	w-s	1.5	
Eragrostis neesii	Poaceae	N	w-s	0.5	
Calamagrostis alba	Poaceae	N	c-s		2.5
Bromus auleticus	Poaceae	N	c-s		1
Aristida murina	Poaceae	N	w-s		2.5
Setaria parviflora	Poaceae	N	w-s		2
Leptocoryphium lanatum	Poaceae	N	w-s		1
Gymnopogon grandiflorus	Poaceae	N	w-s		0.5
Forbs					
Apium leptophyllum	Apiaceae	N	c-s	3	0.5
Baccharis coridifolia	Asteraceae	N	w-s	1	1
Cuphea glutinosa	Asteraceae	N	w-s	0.5	0.5
Dichondra sericea	Convolvulaceae	N	w-s	0.5	0.5
Eryngium horridum	Apiaceae	N	Undef.*	1.5	2
Gamochaeta sp.	Asteraceae	N	c-s	2	
Plantago berroi	Plantaginaceae	N	c-s	2	
Chevreulia sarmentosa	Asteraceae	N	c-s	1.5	

Table 2. (Continued)

Species	Family	Origin	F.G.	Mean frequency	
				G	U
Eryngium nudicaule	Apiaceae	N	c-s	1.5	
Adesmia bicolor	Fabaceae	N	c-s	0.5	
Micropsis spathulata	Asteraceae	N	c-s	0.5	
Oxalis sp.	Oxalidaceae	N	c-s	0.5	
Polygala australis	Polygaleaceae	N	c-s	0.5	
Relbulnium richardianum	Rubiaceae	N	c-s	0.5	
Soliva pterosperma	Asteraceae	N	c-s	0.5	
Sisyrinchum sp.	Iridaceae	N	c-s	0.5	
Richardia humistrata	Rubiaceae	N	w-s	2	
Evolvulus sericeus	Convolvulaceae	N	w-s	1.5	
Achyrocline satureioides	Asteraceae	N	w-s	0.5	
Ambrosia tenuifolia	Asteraceae	N	w-s	0.5	
Glandularia selloi	Verbenaceae	N	w-s	0.5	
Hipochoeris radicata.	Asteraceae	E	w-s	0.5	
Lucilia acutifolia	Asteraceae	N	w-s	0.5	
Pavonia glechomoides	Malvaceae	N	w-s	0.5	
Phyla nodiflora	Verbenaceae	N	w-s	0.5	
Richardia stellaris	Rubiaceae	N	w-s	0.5	
Verbena montevidensis	Verbenaceae	N	w-s	0.5	
Lathyrus subulatus	Fabaceae	N	c-s		1.5
Chaptalia piloselloides	Asteraceae	N	c-s		0.5
Cliococca selaginoides	Linaceae	N	c-s		0.5
Desmanthus virgatus	Fabaceae	N	c-s		0.5
Aspilia montevidensis	Asteraceae	N	w-s		1.5
Tragia pinnata	Euphorbiaceae	N	w-s		1
Vernonia flexuosa	Asteraceae	N	w-s		1
Pfaffia tuberosa	Amaranthaceae	N	w-s		0.5
Shrubs					
Discaria americana	Rhamnaceae	N	c-s	1	0.5
Baccharis trimera	Asteraceae	N	w-s	4.5	8
Eupatorium buniifolium	Asteraceae	N	w-s	4.5	13.5
Baccharis articulata	Asteraceae	N	w-s		0.5
Baccharis dracunculifolia	Asteraceae	N	w-s		0.5
Baccharis spicata	Asteraceae	N	w-s		0.5
Schinus sp.	Anacardiaceae	N	w-s		0.5

Origin: N and E, native and exotic species respectively; F.G., functional group: c-s, cool-season and w-s, warm-season species.
*Undefined cycle.

the grazed area, that occurred mainly during the warm growing period, could be ascribed to the dominance of the cool-season forbs, which may substantially reduce the availability of soil water and nutrients for the warm-season grasses. Mowing of the exclosure did not revert the difference of ANPP between the grazed and the ungrazed situation, reinforcing the idea of a strong component of species composition/diversity mediating the effects of grazing on ANPP.

In contrast, mowing of the exclosure in the Uruguayan Campos reverted the differences observed between G and U: ANPP inside the exclosure became higher than outside, which suggests a stronger component of canopy structure mediating the effects of grazing on ANPP.

The observed twofold increase of ANPP as a result of clipping is one of the highest records of overcompensation ever recorded in the field (see Oesterheld et al. 1999 for a review). Two possible mechanisms related to resource availability may explain this pattern. First, the large amount of standing dead biomass in U probably reduced the absorption efficiency of radiation due to self-
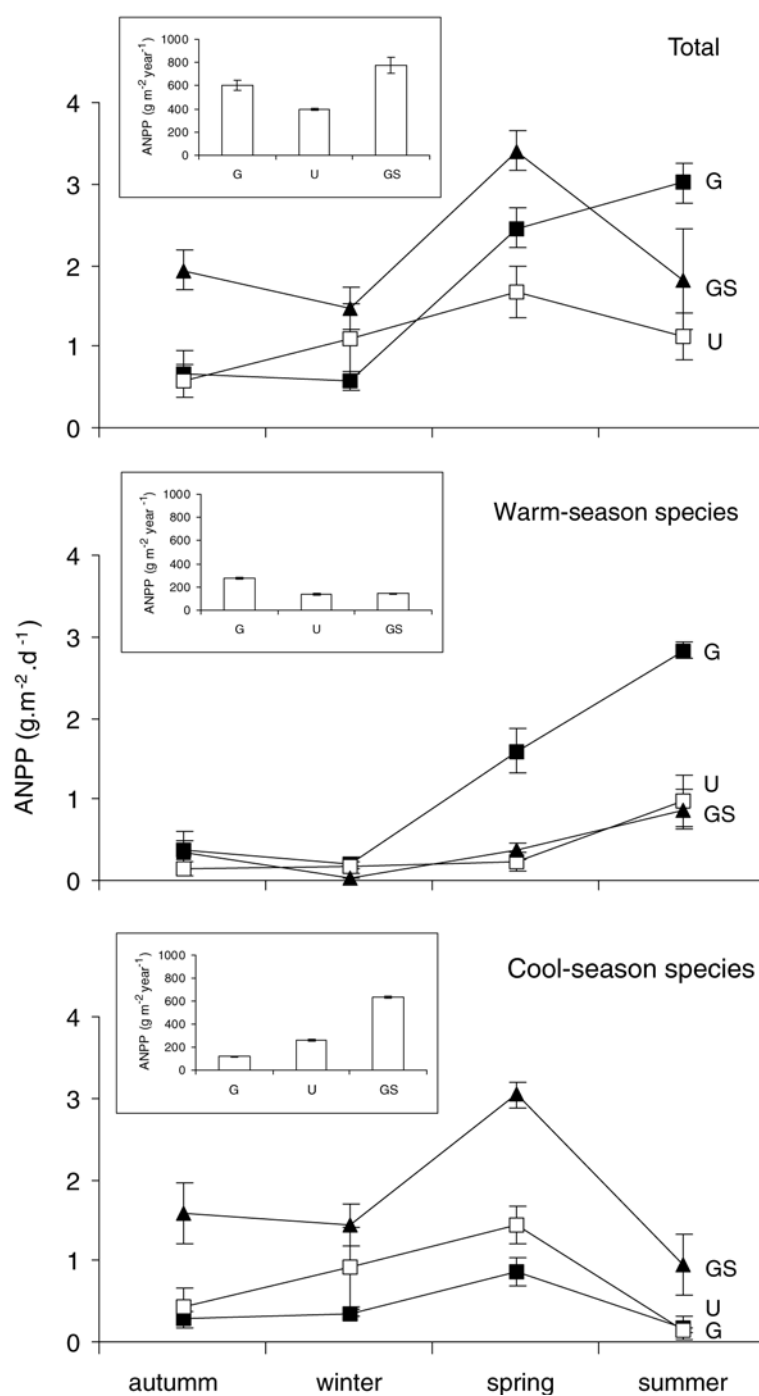
Figure 1. Seasonal and annual ANPP of the entire community (total), the warm-season species, and the cool-season species in each treatment: grazed (G), ungrazed (U) and grazing-simulated (GS) plots. Error bars indicate ±1 SE of the means.

shading (McNaughton 1983b; Oesterheld and McNaughton 1991). Clipping drastically reduced this dead biomass, and thus light interception by green leaves likely increased. Many authors have pointed out that light is one of the most important resources that limit plant production in humid and
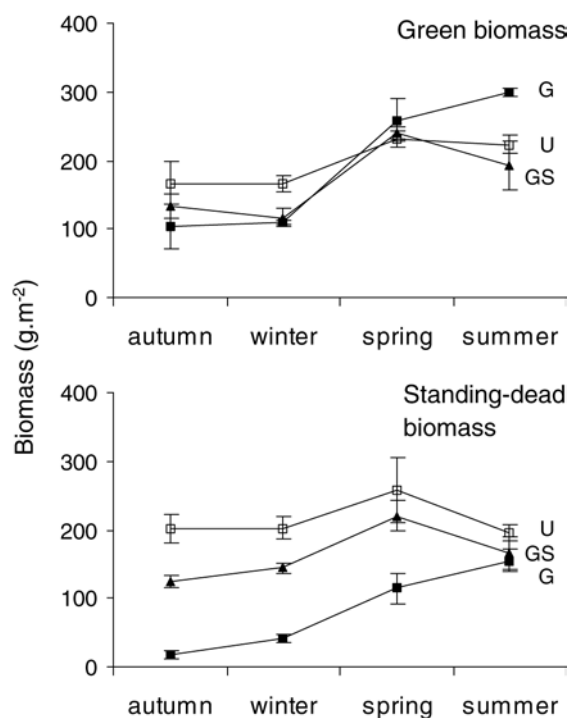
Figure 2. Seasonal green and standing dead biomass for each treatment: grazed (G), ungrazed (U) and grazing-simulated (GS) plots. Error bars indicate ±1 SE of the means.

subhumid grasslands (Semmartin and Oesterheld 1996; Knapp et al. 1998). Second, the removal of standing dead biomass may have increased surface temperature, particularly in winter and autumn. Lower temperatures of the intact exclosure may have reduced ANPP both directly, by limiting plant growth, and indirectly, by reducing the rate of N mineralization (as in Knapp and Seastedt 1986). Additionally, clipping may have altered plant allocation patterns towards higher production of new leaves (Caldwell et al. 1981; Holland et al. 1992). A change in the mean age of the canopy would also increase the photosynthetic efficiency of leaves (McNaughton 1983b).

Compared to clipping, actual grazing reduced rather than increased ANPP. Several mechanisms may be postulated for this response, but they should consider one of the most drastic differences between the grazed plots and the exclosure: the phenological and habit shift associated with the species replacement. During spring and summer the productivity in the grazed area was mainly accounted by warm-season species. A large proportion of them are

prostrate species that concentrate their biomass near the ground. In the GS treatment, on the contrary, cool-season species with erect growth habit seemed to be responsible for the increased ANPP during most of the year (Figure 1). Thus, the species change induced by grazing may have resulted in lower production simply due to a change in environmental conditions associated to seasonality (e.g., lower water availability in summer), or to a compaction of the vertical distribution of leaf area, which lowered the interception of radiation by the canopy (Chapin et al. 2002).

Our results suggest two components of grazing effect that may be postulated for this grassland. The structural component results in higher ANPP, probably due to the elimination of standing dead biomass. The species composition component results in lower ANPP once the structural component is controlled, probably due to the shift to warm-season phenology and prostrate habit. This shift results in several changes that may have potentially reduced ANPP, some related with the availability of resources, while others related with utilization efficiency. Our observations and manipulations are far from singling out the effect of diversity on ecosystem function, something that has proved difficult even in the most controlled situations (Naeem and Wright 2003). However, when biodiversity varies in nature, it covaries with many factors just as in our study. Here we have shown that the direction of ANPP responses to changes in diversity induced by grazing is highly sensitive to the system being observed (Flooding Pampa vs. Campos), and to the structural and species-specific traits that are affected by grazing (standing dead biomass, phenological plant functional groups).

Acknowledgements

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