

## Litter quality and nutrient cycling affected by grazing-induced species replacements along a precipitation gradient

María Semmartin, Martín R. Aguiar, Roberto A. Distel, Alicia S. Moretto and Claudio M. Ghersa

Semmartin, M., Aguiar, M. R., Distel, R. A., Moretto, A. S. and Ghersa, C. M. 2004. Litter quality and nutrient cycling affected by grazing-induced species replacements along a precipitation gradient. – *Oikos* 107: 148–160.

One of the potential mechanisms for the impact of herbivores on nutrient cycling is the effect of selective grazing on litter quality through changes in species composition. However, the scarce evidence collected on this mechanism is controversial and seemingly influenced by site-specific variables. In this paper, we explored the consequences of grazing-induced changes in species composition on litter quality and nitrogen cycling with a regional perspective. Along a 900-mm of mean annual rainfall gradient, we selected species promoted and diminished by grazing from three natural rangelands of Argentina, analyzed their litter quality, and determined their decomposition and nutrient release kinetics under common greenhouse conditions. Litter quality and decomposition rates were strongly associated with plant response to grazing. However, the magnitude and direction of these differences depended on the ecosystem considered. In the wettest site, the species promoted by grazing (forbs) had higher nitrogen and phosphorus contents, faster decomposition rates, and higher release of nitrogen to the soil than species diminished by grazing ( $C_3$  and  $C_4$  grasses). In the intermediate and dry sites, species promoted by grazing had lower nitrogen and phosphorus contents, and slower decomposition rates than those diminished by grazing ( $C_3$  grasses in both cases). Decomposition of the entire group of species was not correlated with mean annual rainfall, but when litter of the species diminished by grazing was analyzed, it was negatively correlated with precipitation. Nitrogen was immobilized more often than mineralized, even after one year of incubation. Immobilization was negatively correlated with precipitation. All these results indicate that grazing may significantly alter nutrient cycling by affecting litter quality through changes in species composition. These effects seem to be larger when species replacements induced by grazing either involve functional groups, as it was the case in our wettest site, or change root to shoot ratios. Therefore, the functional groups involved in the replacement of species as well as shifts between belowground and aboveground allocation should play a key role in grazing-induced changes on nitrogen cycling.

*M. Semmartin, M. R. Aguiar and Claudio M. Ghersa, Cátedra de Ecología, IFEVA, Facultad de Agronomía, Univ. de Buenos Aires, CONICET. Av. San Martín 4453, AR-C1417DSE Buenos Aires, Argentina (semmartin@ifeva.edu.ar). – R. A. Distel, Depto de Agronomía, CERZOS, Univ. Nacional del Sur, CONICET, AR-8000 Bahía Blanca, Argentina. – A. S. Moretto, Centro Austral de Investigaciones Científicas, CONICET, CC.92, AR-9410 Ushuaia, Argentina.*

Plant litter quality affects ecosystem functioning by changing the balance between nutrient release and uptake by decomposers. Plant species are a strong source of variation of litter quality due to their wide range of

arrangements of tissue components (nitrogen, phosphorus, lignin, secondary compounds) even within a particular community, a functional group, or a botanical family (Enriquez et al. 1993, Cornelissen 1996, Grime et

Accepted 19 February 2004

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ISSN 0030-1299

al. 1997). Litter quality has been proposed as a strong driver of decomposition rates and nutrient release, together with climate and soil properties (Swift et al. 1979, Melillo et al. 1982, Wedin and Tilman 1990, Hobbie 1992, Enriquez et al. 1993, Vinton and Burke 1995). For a given climate–soil combination, decomposers release or immobilize nutrients according to the absolute and relative contents in litter which, in turn, change during decomposition (Aber and Melillo 1991). In general, it is accepted that lower carbon to nitrogen ratios promote nutrient release, whereas higher ratios induce microbial immobilization (Aber and Melillo 1991).

In temperate grasslands, litter quality varies as a consequence of two major forces: mean annual rainfall and grazing regime. A number of studies showed that litter quality traits, such as carbon to nitrogen or lignin to nitrogen ratios, consistently increase along precipitation gradients from arid through humid ecosystems (Bremner and de Wit 1983, Parton et al. 1987, Wedin 1994, Burke et al. 1997, Murphy et al. 2002). Grazing has the potential to affect litter quality through its well-documented effects on plant species composition (Milchunas and Lauenroth 1993). These effects may be highly relevant to ecosystem functioning, since the amount of soil nitrogen derived from plant litter in grazed grasslands can be 2 to 8 times greater than nitrogen derived from urine and feces (Holland et al. 1992, Chaneton et al. 1996). Surprisingly, changes in litter quality and nutrient cycling produced by grazing-induced changes in species composition are far from clear. For example, Pastor et al. (1993) found that moose browsing in a boreal forest diminished soil nitrogen mineralization by promoting less palatable and less decomposable tree species. Similar results were found in an oak savanna, but the reduction of a palatable legume species by selective grazing appeared to be responsible for the lower nitrogen mineralization in the grazed sites (Ritchie et al. 1998). Instead, in a tundra heath ecosystem, Olofsson and Oksanen (2002) found that grazing by reindeer promoted grasses that decomposed faster than the dominant shrubs of lightly grazed sites.

This disparity of responses to grazing may be partially driven by an interaction between climate and grazing impacting on nutrient cycling through changes in species composition, which has not been explored so far. At a regional scale, grassland species composition is interactively influenced by a strong covariance of precipitation and grazing regime. As mean annual precipitation increases, so does plant cover, species diversity, height, and productivity (McNaughton 1983, Sala et al. 1988, Coupland 1992). All these structural and functional changes are accompanied by a gradual replacement of species. Additionally, grazing intensity, expressed as the proportion of plant productivity consumed by herbi-

vores, also increases (McNaughton et al. 1989), and affects community structure and species composition (Milchunas and Lauenroth 1993). Therefore, these two forces, rainfall and grazing, appear to be major drivers of vegetation traits, some of which are clearly associated with litter quality.

As a result of this covariance, floristic changes induced by grazing vary with climate. Evidence indicates that changes in species composition induced by grazing are more pronounced as rainfall or productivity increase (Milchunas and Lauenroth 1993). This pattern has been attributed to the fact that many traits that confer resistance to herbivory also enhance the ability to resist water limitations via tolerance and/or avoidance (Coughenour 1985). Examples of these traits are plant small stature, basal meristems, high shoot density, deciduous shoots with senescent leaves, and lignin and silica content (Coughenour 1985). In contrast, traits such as plant height and allocation to aboveground growth confer a greater ability to compete for light and a lower grazing resistance (Sims and Singh 1978, Coughenour 1985, Milchunas and Lauenroth 1993). Therefore, the smaller species changes induced by grazing in drier sites and the convergence of traits that confer resistance to drought and grazing suggest that litter quality and its consequent effect on nutrient cycling will be less affected by grazing-induced changes in species composition in drier sites than in more humid sites. However, there is no direct empirical evidence for this pattern.

In this paper we investigated the consequences of grazing-induced species changes on litter quality and its relationship with decomposition and nutrient cycling in three grasslands encompassing a wide range of mean annual precipitation. We first studied the litter chemistry of species promoted and diminished by grazing in three communities located along a 900-mm precipitation gradient in temperate South America. We then estimated decomposition rate and nutrient release rate for the species under common, non-limiting conditions. We also studied soil mineral nitrogen dynamics in samples amended with this litter.

## Material and methods

### Study sites and litter collection

The three ecosystems studied here are distributed along a mean annual rainfall gradient that ranges from 150 mm to 1000 mm. These ecosystems have been subjected to extensive domestic grazing (mainly cows and sheep) during the last few centuries, which resulted in well-documented species replacements (Soriano 1992, Llorens 1995).

The driest ecosystem is the Occidental Phytogeographical District of the Patagonian grass–shrub steppe (Soriano 1983, León et al. 1998). The species used in the

present study were collected at the Río Mayo experimental site, 45°S, 70°W. Mean annual rainfall is 170 mm concentrated in fall and winter. Mean monthly temperatures range from 2°C in July to 14°C in January. Soils are derived from glacial and volcanic materials, and are coarse textured with a petrocalcic horizon at 60 cm depth (Paruelo et al. 1988). We studied four species: two bunchgrasses, largely preferred by grazers, which reduce their abundance with increasing grazing intensity (G–): *Bromus pictus* Hook f. and *Poa ligularis* Nees ap. Steud., and two bunchgrasses with an opposite response to increasing grazing intensity (G+): *Stipa speciosa* Trin. et Rupr. and *S. humilis* Cav. The selected grasses not only exhibit a clear response to grazing but also represent a significant proportion of total plant abundance. For instance, whereas in ungrazed sites *Poa* and *Bromus* together account for 11% of total plant cover, in grazed and overgrazed sites their cover, particularly *Bromus*, decrease by five fold (Soriano et al. 1994, Perelman et al. 1997, Aguiar et al. 1999). In the case of *Stipa*, both species account for over 40% of the total plant cover in grazed areas (Golluscio et al. 1982), whereas they reached approximately 12% in ungrazed paddocks (Soriano et al. 1994, Perelman et al. 1997).

The Caldenal semi-arid grassland is the ecosystem in the middle of the precipitation gradient, which belongs to the Calden Phytogeographical District (Cabrera 1976). The dominant vegetation type of this district is grassland with isolated woody plants (*Prosopis caldenia*). The grass layer is dominated by perennial cool-season bunchgrasses (Distel and Bóo 1996). The species analyzed in this study were located in an upland site at 38°S, 63°W. Mean annual rainfall is 550 mm, with peaks in fall and spring and drought during summer. Mean monthly temperatures range from 7°C in July to 24°C in January. Soils are coarse textured Calciustolls, with a petrocalcic horizon at 60–80 cm depth. The species selected from this site were two G– bunchgrasses *Stipa clarazii* Ball. and *Poa ligularis*, and two G+ bunchgrasses *Stipa tenuissima* Trin. f. and *S. gynerioides* Phil. (Cano 1975, Bóo et al. 1993). *Poa* is the dominant species of the herbaceous layer in ungrazed condition (Llorens 1995) whereas its contribution to plant biomass in grazed and overgrazed sites is negligible (<1%, Pisani et al. 2000). The two G– species are highly preferred by herbivores since their relative abundance in the animals diet increase between 2 to 70 fold their relative abundance in the pasture (Pisani et al. 2000). Instead, the two G+ *Stipas*, which together account for >50% of the plant biomass in grazed areas, are not detected in the animals diet (Pisani et al. 2000).

The most humid ecosystem was the Flooding Pampa grasslands. The species analyzed here belong to a site located at 36°S, 58°W, which receives a mean annual rainfall of approximately 1000 mm uniformly distributed

throughout the year. Mean monthly temperatures range from 7°C to 22°C, and soils are typical natraquoll, which are frequently waterlogged during winter and early spring. We concentrated in stands of the most widespread community classified as a humid mesophytic meadow (Perelman et al. 2001). The G– species selected from this site were two bunchgrasses, *Danthonia montevidensis* Hack. et Arech. and *Bothriochloa laguroides* D.C., a cool season and a warm season species respectively; since there are no grasses clearly promoted by grazing in this region (Chaneton et al. 2002), we selected two G+ exotic herbs that become dominant in grazed areas: *Mentha pulegium* L. and *Leontodon taraxacoides* Vill. (Sala et al. 1986). In ungrazed sites, *Danthonia* and *Bothriochloa* account for ~25% of the aerial net primary productivity, during their peak biomass periods (Sala et al. 1981). In these grasslands, grasses cover decreases with grazing from 70% in ungrazed condition to 20% in grazed sites (Chaneton et al. 2002). Instead, the forbs studied in this experiment, which are virtually absent in ungrazed condition, account for >60% of plant cover in grazed sites (Chaneton et al. 2002).

Litter from Patagonia and Caldenal was collected in situ during spring, in sites fenced to exclude large herbivores. We collected entire tussocks (with roots attached) for further harvest of recently senesced above-ground biomass, and roots. Since in situ litter collection of the species from the Flooding Pampa was virtually impossible, due to high grazing intensity, we collected individual plants in soil monoliths, during the spring before the experiment, and grew them at the School of Agronomy Campus in Buenos Aires, which is in the same region (approximately 200 km from the field). Aboveground litter was collected during the spring on a daily basis, and live and senescent roots were collected in a destructive harvest at the end of the growing period, immediately before the beginning of the determinations of litter chemistry and the experiment described below.

### Initial litter chemistry

We compared the content of nitrogen, phosphorus, and lignin in the aboveground litter and roots of all species. Three samples of each species and tissue type were milled, and 100 mg were digested with a mix of sulfuric acid, cupric and potassium sulfate, and hydrogen peroxide at 300°C for an hour. Digests were analyzed by a colorimetric technique with a flow injection auto-analyzer (Alpkem Corporation, Wilsonville, Oregon) to measure nitrogen and phosphorus contents. Another 500 mg aliquot of the milled samples was used to determine lignin content (Van Soest and Wine 1968). Placed inside porous crucibles, it received successive digestions with 100 ml of acid detergent solution at

100°C, and with sulfuric acid 70% m/v at room temperature. The digests were washed with acetone and hot distilled water with the help of a vacuum pump, dried at 70°C, and weighed. The remaining masses inside the crucibles were ashed at 500°C and weighed.

## Experimental design and assembly of litter bags and soil microcosms

An experiment was conducted to evaluate species effects on decomposition, litter nutrient release, and soil mineral nitrogen dynamics. The basic design was a two-way factorial design of litter type and harvest date (24 litter types which stemmed from aboveground and root tissue of 12 species, and five dates: 0, 30, 100, 180, and 365 days). In order to investigate particular aspects of the experiment, we classified the litter types according to species response to grazing (G+ and G−, grazing promoted and diminished respectively), origin site (dry, intermediate, and wet), and tissue (aboveground and roots). The experimental units were soil microcosms (below) that contained a single nylon bag with one litter type. There were three replicates per litter type and harvest date, and three additional empty bags were harvested each date as a blank control (total = 375 microcosms).

The assembly of litter bags and soil microcosms was based on the protocol described by Hobbie (1996). Previously washed and air-dried litter was sectioned in small pieces (2 cm long approximately) and a known amount (approximately 1 g) of each litter type was enclosed within a 60 cm<sup>2</sup> nylon bag (0.35 mm mesh). Bags with roots of *L. taraxacoides* and *M. pulegium* were filled with approximately 0.5 g because of difficulties to collect more material. Individual 10 × 15 cm plastic boxes (soil microcosms) containing 15 g of dry soil, and watered up to field capacity were amended with the litter bags. Soil was the same for all the incubations and was collected from the upper horizon of the Flooding Pampa grasslands. It was previously sieved in order to remove plant and animal debris. It was homogenized by hand, moistened up to field capacity and incubated in the dark for 2 weeks. Before the amendments, soil microcosms were washed with 100 ml of distilled water at a rate of 6 ml per minute, in order to homogenize them and wash the excess of nutrients in soil solution. During the incubation of the litter bags, the microcosms were kept in a greenhouse under dark conditions, and with regulated temperature at 20–25°C. Soil moisture was maintained by weekly spraying distilled water. The microcosms were arranged randomly and rotated with a decreasing frequency during the experiment, once a month in average, to avoid variability due to any environmental gradient within the greenhouse.

After each harvest, a 10 g sample of wet soil was extracted with 50 ml of 2 mol/l KCl for colorimetric determination of NH<sub>4</sub>-N and NO<sub>3</sub>-N content, and another sample was dried for gravimetric moisture content (70°C). Harvested litter was carefully brushed and washed to remove soil particles. It was air dried for 4 days to constant weight and weighed. Samples were milled and a 100 mg sub-sample was used to determine total nitrogen and phosphorus contents as described above.

## Decomposition rate estimation and statistical analyses

In order to correlate litter decomposition rates with measures of litter quality we calculated a litter decay constant “k” as the slope of a single exponential decay model for each litter type (Olson 1963, Wieder and Lang 1982, Hobbie 1996):  $\ln(M_t/M_0) = -kt + c$ ; where  $M_t$  and  $M_0$  are remaining masses at time  $t$  and 0 respectively,  $t$  is time in days and  $c$  is a regression constant. The models were derived by least-squares regressions. Data corresponding to initial litter quality were analyzed by a three-way ANOVA with response to grazing, origin site, and tissue as factors (Zar 1999). ANOVAs were followed by LSD tests. Data corresponding to remaining litter mass, soil nitrogen content, and nitrogen and phosphorus contents in remaining litter were analyzed by two-way ANOVAs with litter type and harvest time as factors, and by three-way ANOVAs to detect response to grazing, origin site, and tissue effects. The level of statistical significance was 0.05, unless otherwise specified in the text.

## Results

### Initial litter chemistry

Initial litter chemistry showed large differences that were interactively accounted for by species response to grazing, origin site, and tissue (Table 1, 2). The differences due to species response to grazing depended on site. In the wet site, litter of G+ species (forbs) was richer in nitrogen and phosphorus than litter of G− species (grasses, Table 1, 2). In contrast, litter of G+ species had the same and lower nitrogen and phosphorus contents than litter of G− species in the dry and intermediate sites respectively (Table 1, 2). Nitrogen and phosphorus content varied among systems but interactively with response to grazing and tissue: G+ forbs from the wet site had significantly larger nitrogen and phosphorus content than the rest while aboveground litter of G− species from the dry site had the lower contents of nitrogen (Table 1, 2). Nitrogen and phosphorus content showed significant differences be-

Table 1. Initial chemical characteristics of litter. G – and G+ mean species diminished and promoted by grazing respectively.

Species	Response to grazing	Nitrogen (%)		Phosphorus (%)		Lignin (%)	
		Aboveground	Roots	Aboveground	Roots	Aboveground	Roots
Drysite							
<i>Bromus pictus</i>	G –	0.52 (0.01)	0.70 (0.05)	0.06 (0.0005)	0.10 (0.001)	5.13 (0.65)	12.58 (0.27)
<i>Poa ligularis</i>	G –	0.29 (0.03)	0.53 (0.02)	0.03 (0.003)	0.05 (0.002)	3.82 (0.31)	12.42 (0.45)
<i>Stipa humilis</i>	G +	0.42 (0.02)	0.61 (0.03)	0.03 (0.003)	0.08 (0.001)	6.75 (0.57)	14.70 (0.83)
<i>Stipa speciosa</i>	G +	0.27 (0.01)	0.55 (0.05)	0.02 (0.0002)	0.08 (0.002)	8.58 (0.75)	14.36 (0.25)
Intermediate site							
<i>Stipa clarazii</i>	G –	0.84 (0.04)	0.57 (0.003)	0.07 (0.01)	0.06 (0.002)	4.97 (0.52)	12.29 (0.43)
<i>Poa ligularis</i>	G –	0.63 (0.02)	0.40 (0.03)	0.06 (0.01)	0.06 (0.01)	4.03 (0.42)	10.82 (0.47)
<i>Stipa gynerioides</i>	G +	0.58 (0.06)	0.40 (0.03)	0.04 (0.002)	0.02 (0.006)	9.20 (0.66)	15.29 (0.30)
<i>Stipa tenuissima</i>	G +	0.47 (0.04)	0.51 (0.10)	0.03 (0.01)	0.03 (0.015)	7.41 (0.44)	11.98 (0.59)
Web site							
<i>Danthonia montevidensis</i>	G –	0.68 (0.08)	0.75 (0.04)	0.04 (0.01)	0.06 (0.004)	5.78 (0.38)	13.84 (0.11)
<i>Bothriochloa laguroides</i>	G –	0.77 (0.01)	0.56 (0.05)	0.04 (0.01)	0.04 (0.01)	5.48 (0.33)	13.02 (0.49)
<i>Leontodon taraxacoides</i>	G +	2.32 (0.19)	1.81 (*)	0.35 (0.04)	0.16 (*)	4.40 (0.41)	12.6 (*)
<i>Mentha pulegium</i>	G +	2.27 (0.04)	1.73 (*)	0.25 (0.01)	0.14 (*)	4.41 (0.33)	11.46 (*)

SE in parenthesis; (\*) pooled samples.

tween roots and aboveground litter but they depended on the site: in the driest site, roots showed higher contents than aboveground tissue, whereas in the other two sites the opposite pattern was observed (Table 1, 2).

Lignin content differed significantly among species response to grazing, origin site, and tissue. The differences due to response to grazing depended on the origin site (Table 1, 2). Lignin content was higher in the G+ than in the G – species in dry and intermediate sites whereas the opposite was observed in the wet site (Table 1, 2). In contrast to the pattern observed for nitrogen and phosphorus, lignin content of the wet site species appeared more homogeneous compared to the species from the other sites. This is particularly remarkable since the species from the wet site included forbs, C<sub>3</sub> and C<sub>4</sub> grasses while species from the intermediate and dry sites were all C<sub>3</sub> grasses. Lignin content varied among sites but did so interactively with the response to grazing as G+ species from the wet site had lower content whereas G – species did not show differences among sites (Table 1, 2). Roots of the three sites had greater lignin contents than aboveground litter (Table 1, 2).

## Litter decomposition

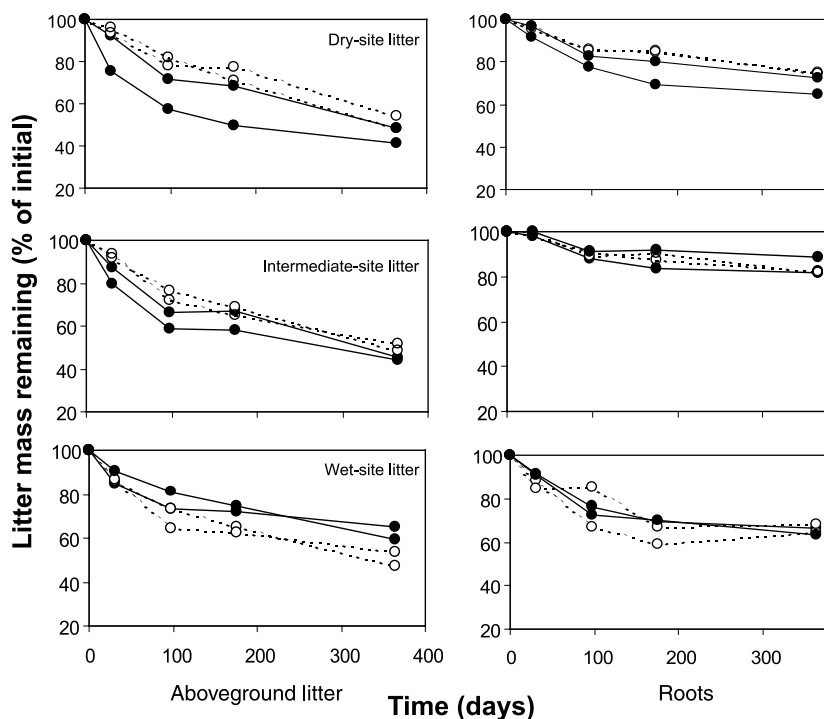
There were large differences in litter decomposition dynamics interactively accounted for by response to grazing, origin site, and tissue. Relative decomposition rate of litter (k) ranged from 0.1 to 0.8 (Table 3), which means that the remaining biomass after one year of incubation ranged from 75% to 45% of the initial biomass (Fig. 1). Response to grazing explained differences of decomposition, but the pattern depended on the site considered ( $P_{\text{grazing} \times \text{site}} < 0.001$ ; Table 3, Fig. 1): mass loss was significantly greater in G – than in G+ species from the intermediate and dry sites, whereas the opposite pattern was observed in species of the wet site.

Regarding the differences observed along the precipitation gradient, decomposition varied among sites interactively with response to grazing and tissue ( $P_{\text{site} \times \text{grazing}} < 0.001$ ;  $P_{\text{site} \times \text{tissue}} < 0.0001$ ), which indicates a non-consistent pattern of litter decomposability across the gradient. Aboveground litter of G – species from the intermediate and dry sites decomposed significantly faster than from the wet site. In contrast, an opposite pattern was observed for roots. In the wet site, there was a sharp contrast between the slow decomposi-

Table 2. Multifactor ANOVA results for initial tissue chemistry of litter.

Source	Nitrogen			Phosphorus			Lignin		
	F ratio	df	P-value	F ratio	df	P-value	F ratio	df	P-value
Grazing	156	1,56	0.001	45	1,56	0.001	26	1,56	0.001
Origin site	282	2,56	0.001	54	2,56	0.001	3,4	2,56	0.038
Tissue	6	1,56	0.014	2.5	1,56	0.11	660	1,56	0.001
Grazing × Origin site	151	2,56	0.001	76	2,56	0.001	21	2,56	0.001
Grazing × Tissue	1.4	1,56	0.23	9.9	1,56	0.002	3.4	1,56	0.07
Origin site × Tissue	13	2,56	0.001	19	2,56	0.001	3.1	2,56	0.056
Grazing × Site × Tissue	8.1	2,56	0.001	14	2,56	0.001	0.6	2,56	0.55

Fig. 1. Litter decomposition dynamics of grazing diminished species (G–) ●; and grazing promoted species (G+) ○ of the three grasslands. Left panels correspond to aboveground litter and right panels to roots.



tion rate of aboveground litter of G– species and the fast decomposition rate of both the roots of this same group and all material of the G+ group (Table 3, Fig. 1).

Regarding tissue effects, roots had a slower decomposition rate than aboveground litter, but the difference diminished toward the wet end of the gradient ( $P_{\text{tissue} \times \text{site}} < 0.0001$ ), where there was no significant difference between aboveground litter and roots ( $P = 0.28$ , Table 3, Fig. 1).  $k$  of the entire set of

incubations was negatively correlated with initial lignin content and lignin to nitrogen ratio (Fig. 2). The major source of variation for these key quality variables was tissue type, since roots had a much higher lignin content and, occasionally, a lower nitrogen content, than aboveground litter. There was also a significant negative correlation between  $k$  and lignin to nitrogen ratio within roots, while aboveground litter  $k$  was not correlated with any of these parameters of quality.

Table 3. Decomposition rates of different litter types. G– and G+ mean species diminished and promoted by grazing respectively. Least significant difference = 0.038.

Species	Response to grazing	K (year <sup>−1</sup> )			
		Above ground	SE	Roots	SE
Dry-site litter					
<i>Bromufi pictus</i>	G −	0.79	0.10	0.42	0.06
<i>Poa ligularis</i>	G −	0.72	0.06	0.32	0.04
<i>Stipa humilis</i>	G +	0.58	0.03	0.29	0.03
<i>Stipa speciosa</i>	G +	0.74	0.04	0.28	0.03
Intermediate-site litter					
<i>Stipa clarazii</i>	G −	0.74	0.10	0.12	0.03
<i>Poa lisularis</i>	G −	0.74	0.06	0.21	0.03
<i>Stipa gynerioides</i>	G +	0.65	0.05	0.21	0.02
<i>Stipa tenuissima</i>	G +	0.71	0.05	0.20	0.02
Wet-site litter					
<i>Danthonia montevidensis</i>	G −	0.49	0.03	0.42	0.07
<i>Bothriochloa laguroides</i>	G −	0.37	0.06	0.39	0.06
<i>Leontodon taraxacoides</i>	G +	0.81	0.20	0.42	0.14
<i>Mentha pulegium</i>	G +	0.57	0.10	0.36	0.09

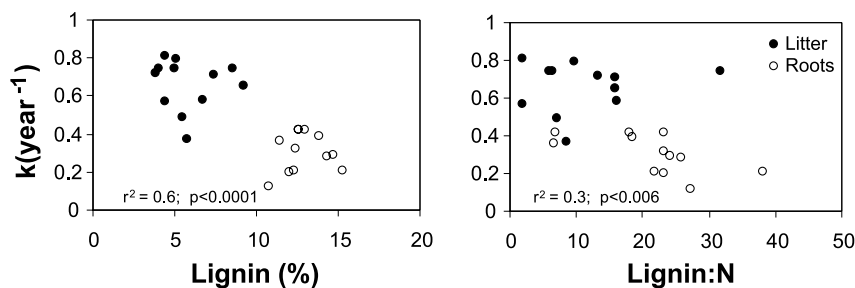


Fig. 2. Relationship between litter decomposition rate ( $k$ ) and initial lignin content (left panel), and lignin:N ratio (right panel).

### Nutrients dynamics in litter

Litter types differed significantly in their nitrogen release patterns and that variation was interactively accounted for by response to grazing, origin site, and tissue (Fig. 3). In general, results ranged from a net immobilization to a slight net mineralization during several periods. Response to grazing affected the nitrogen pattern release of species from the wet site ( $P_{\text{grazing} \times \text{site}} < 0.0001$ ), where nitrogen was more immobilized in G – species (grasses) than in the G+ species (forbs), which showed net nitrogen mineralization throughout the total incubation period (Fig. 3). Instead, aboveground litter of G+ species from the intermediate site had greater immobilization than the G – species, whereas species

from the dry site showed no differences in their nutrient release accounted for by grazing, but showed differences among species. Aboveground litter of *Bromus pictus* immobilized significantly less nitrogen than the rest of this group during the second half of the incubation period. Nitrogen immobilization during the first month was negatively correlated with the mean annual rainfall of the origin site ( $F_{(1,94)} = 39.9$ ;  $P < 0.0001$ ;  $r^2 = 0.3$ ). Differences in nitrogen release between aboveground litter and roots were only significant for Patagonian species, which showed greater immobilization in aboveground litter than in roots ( $P_{\text{tissue} \times \text{site}} < 0.0001$ ). In general, nitrogen immobilization was positively correlated with the initial lignin to nitrogen ratio of the litter ( $F_{(1,22)} = 14$ ;  $P < 0.001$ ;  $r^2 = 0.4$ ).

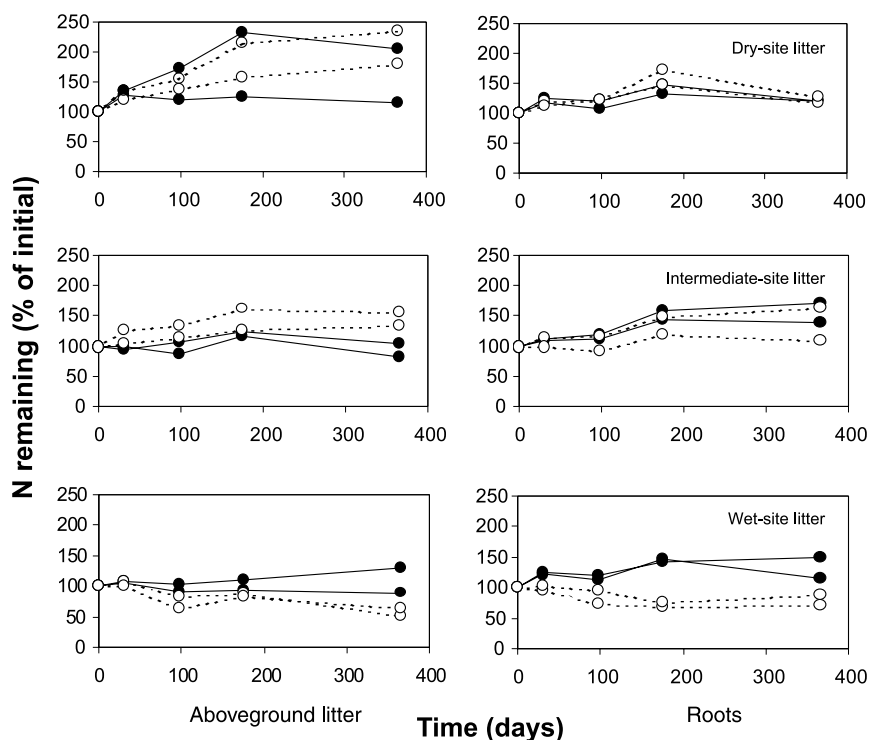


Fig. 3. Decomposition dynamics of nitrogen release for litter of grazing diminished species ●; and grazing promoted species ○ of the three grasslands. Left and right panels correspond to aboveground litter and roots respectively.

Litter phosphorus contents were highly correlated with nitrogen contents ( $F_{(1,94)} = 83$ ;  $P < 0.0001$ ,  $r^2 = 0.47$ ) and thus followed a similar pattern to that of nitrogen (Fig. 4). However, net mineralization of phosphorus throughout the year was more frequent than in the case of nitrogen.

### Nitrogen dynamics in amended soil

Soil nitrogen contents differed in relation to the species response to grazing, origin site, and tissue. As expected from patterns described for previous processes, there were interactions among factors ( $P_{\text{grazing} \times \text{site} \times \text{tissue}} < 0.0004$ ). Soil mineral nitrogen, which was approximately 35 micrograms per gram of soil at the beginning of the experiment, enriched up to 950 micrograms per gram of soil after one year (Fig. 5). Species response to grazing affected soil nitrogen contents differentially among sites ( $P_{\text{grazing} \times \text{site}} < 0.0001$ ): G+ litter from the wet site had dramatically higher nitrogen contents than the G- litter and control incubations. Incubations amended with litter from intermediate- and dry- site species yielded in significantly lower nitrogen contents than control and wet site incubations and did not show differences accounted for by species response to grazing. However, the G- species common to both sites (*Poa ligularis*) had a similar response to the

corresponding G+ species, while the other G- species showed significantly higher nitrogen contents (Fig. 5). Soil nitrogen content differed among sites but interactively with the other factors, as differences appeared strongly explained by the G+ (forbs) of the wet site: *Leontodon taraxacoides* and *Mentha pulegium*. Instead, when considering only the G- species, there were no differences among sites. Incubations amended with aboveground litter from intermediate and dry sites yielded in significantly lower nitrogen contents than root incubations, whereas incubations amended with wet-site species resulted in an inverse pattern ( $P_{\text{tissue} \times \text{site}} < 0.0004$ ), yet this result probably underestimates reality, since, the amount of the G+-root amendment of wet-site species was lower, as previously explained in Methods section. Considering all the time intervals between consecutive harvests, the changes in soil nitrogen contents were negatively correlated with the changes in litter nitrogen, which indicates that the immobilization/mineralization balance at litter level was perceived at the soil level ( $F_{(1,22)} = 20.3$ ;  $P < 0.0002$ ;  $r^2 = 0.48$ ).

### Discussion

Grazing affects ecosystem processes in many different ways. Here, we isolated and studied the effects of species

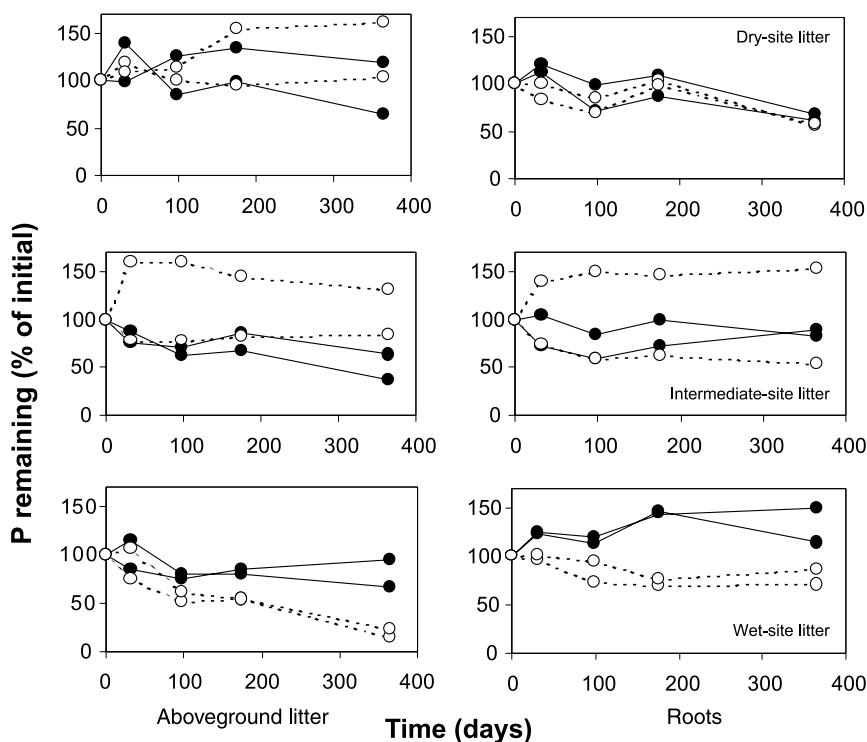


Fig. 4. Decomposition dynamics of phosphorous release for litter of grazing diminished species ●; and grazing promoted species ○ of the three grasslands. Left and right panels correspond to aboveground litter and roots respectively.



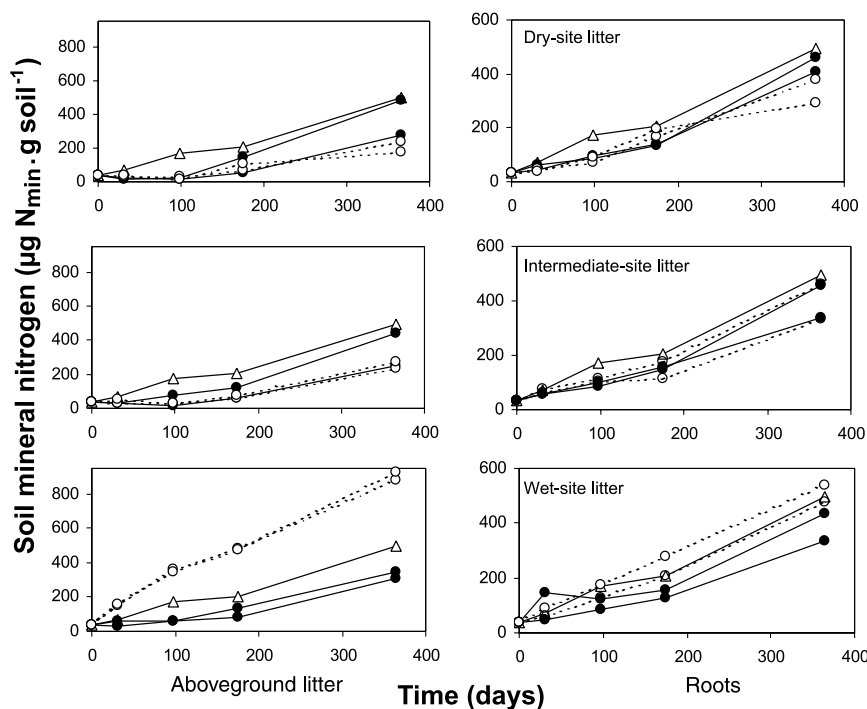


Fig. 5. Soil mineral N dynamics in incubations of control (non-amended soil)  $\Delta$ , grazing diminished species  $\bullet$ , and grazing promoted species  $\circ$  of the three grasslands. Left and right panels correspond to aboveground litter and roots incubations respectively. Note the differences in Y-axis scale between aboveground litter and roots.

change induced by grazing on litter quality and nutrient cycling in species from three rangelands distributed along a 900-mm gradient of mean annual rainfall. We circumscribed our research to two grazing promoted and two grazing diminished species in each rangeland, that account for major proportion of total biomass in grazed and ungrazed conditions respectively. We found that grazing effects may result in different litter quality and decomposition kinetics as well as in nutrient release patterns and soil nutrient availability. However, the magnitude and direction of the potential effects differed among ecosystems: in the intermediate and dry sites, where the most conspicuous species replacement occurs among native grasses, the G+ grasses showed poorer quality (higher lignin to nitrogen ratios), decomposed more slowly, and released less nitrogen and phosphorus to the soil than the G- grasses. In contrast, in the wet end of the gradient, where the most significant replacement is between native grasses and exotic forbs, the promoted forbs showed richer litter quality (lower lignin to nitrogen ratios), decomposed drastically faster, and released more nitrogen and phosphorus to soil than the G- grasses.

Our results agree with the idea that grazing has a greater effect on nutrient cycling as mean annual rainfall increases and as the species change involves greater functional group diversity (Coughenour 1985, Díaz and Cabido 2001). In the intermediate and dry sites, the floristic change induced by grazing involved a single group of C<sub>3</sub> native bunch grasses, whereas in the wet site

involved C<sub>3</sub> exotic forbs replacing native C<sub>3</sub> and C<sub>4</sub> bunch grasses. When the replacement occurred among grasses, the promoted species exhibited traits deterrent to large herbivores, such as higher lignin contents, and low nitrogen concentration, which retarded decomposition and nutrient release. However, this set of traits was just exacerbated in the promoted species, but it was not novel to those ecosystems since they were present in the grazing-diminished grasses (reviewed by Coughenour 1985). Instead, when the promoted species were exotic forbs replacing grasses, the type of herbivore-deterrent traits were prostrated phenotypes, plants with higher concentration of phenolics, alkaloids, and flavonoids, frequently with higher nitrogen content and lower lignin (reviewed by Coughenour 1985), that did not retard nutrient cycling but enhanced it. Many of these traits are not present in the grazing-diminished grasses and then, are novel to the ecosystem and may have a higher chance of causing large changes in ecosystem processes as nutrient cycling (Wardle et al. 1997, Díaz and Cabido 2001).

Milchunas and Lauenroth (1993) provided a global synthesis aimed at relating plant species replacement induced by grazing and several ecosystem features that included total soil nitrogen content. They posed the issue along a gradient of net primary productivity, which is a well accepted surrogate of ecosystem carrying capacity (McNaughton et al. 1989, Oesterheld et al. 1992). The study showed that the magnitude of change in species composition ("dissimilarity") comparing grazed and

ungrazed plots increased with net primary productivity and mean annual rainfall, and less significantly with the evolutionary history and intensity of herbivory. The conceptual model behind these findings proposed that the relative impact of herbivory would be greater in more humid grasslands since the aboveground-to-belowground ratios increase with mean annual rainfall and/or primary productivity (Milchunas et al. 1988). Likewise, the authors explored potential relationships between species change and total soil nitrogen contents and found no correlation. These analyses results are extremely helpful to understand the primary forces driving the impact of grazing on a global basis, as well as to predict with great accuracy the magnitude of changes expected to take place in grasslands. However, the fact that no relationship among dissimilarity and soil nitrogen was found, together with other evidence and the comparative analysis provided in this work suggest that the knowledge of the functional groups involved in the replacements would help to understand and predict the links between grazing and nutrient cycling in such a global perspective. That positive relationship between dissimilarity and primary productivity does not necessarily involve greater functional diversity. It may involve species with complementary effects on ecosystem processes resulting in a moderate final impact (Wardle et al. 1997). Therefore, a redefinition of dissimilarity between grazed and ungrazed areas based on the differences in functional groups (forbs, grasses, shrubs, nitrogen fixers, etc.) rather than in species might reveal a pattern in soil nitrogen availability and primary productivity associated with "functional group dissimilarity".

Published evidence reveals drastic changes in nutrient release and decomposability when grazing causes significant changes in functional diversity, although the species replacement effect might be confounded with other effects of grazing. For example, in a North American semiarid grassland, grazing by prairie dogs and bison promoted the replacement of a few dominant grasses by a wide number of forbs, and soil net nitrogen mineralization was 4 times greater in the grazed, forb-dominated site (Fahnestock and Detling 2002). In contrast, Ritchie et al. (1998) found that in a North American oak savanna, grazing decelerated nitrogen cycling and lowered soil nitrogen availability by reducing the abundance of a palatable legume. So far, empirical evidence is both controversial and incomplete, since many of the studies were not designed to isolate the species-replacement effect from other covariant effects such as plant biomass, primary productivity, trampling by grazers, dung and urine deposition, etc. Unfortunately, empirical evidence from experiments that isolate the species effect from other grazing effects is scarce. A recent study in a tundra heath showed that reindeer induced the replacement of shrubs by grasses with higher litter quality, decomposition rates, and carbon and

nitrogen release from litter (Olofsson and Oksanen 2002). Despite in this example the species replacement was inverse to the one given in our wet site, it represents another evidence of a species replacement involving different functional groups with positive effects on nutrient cycling.

It has been widely accepted that aboveground litter quality decreases with increasing mean annual rainfall and aerial net primary production (Wedin 1994, Austin and Vitousek 2000, Murphy et al. 2002). Moreover, this assumption underlies the most widespread simulation model of nutrient cycling (Parton et al. 1987). Our reduced sub-set of species, in contrast, does not support this idea, neither considering an intensively grazed scenario with a high proportion of G+ species nor a pristine one, with a high proportion of the G- species. Instead, our results suggest that under a scenario of widespread and intense grazing, as it is usually the case in Argentine grasslands, litter quality increases with mean annual rainfall. This notion agrees with a global analysis of grasslands and savannas, based on 61 independent and published data-sets, which did not find any correlation between nitrogen content of green biomass and mean annual rainfall across a similar range of precipitation as the one considered in the present study (Oesterheld et al. 1999).

We found that root litter quality, decomposition and nutrient release were poorly correlated with their aboveground counterpart. This fact prevents us from arriving to general conclusions on ecosystem processes based exclusively on one portion of the system (belowground or aboveground). However, a major proportion of research aimed at understanding nutrient cycling has been devoted to leaf litter decay patterns (Hobbie 1992, Austin and Vitousek 2000, Murphy et al. 2002). This bias results particularly controversial in grassland ecosystems, where root biomass is about 4 to 7 times greater than aboveground biomass, even when only considering roots of the first centimeters of soil, where biological processes are greater (Jackson et al. 1996). Wedin and Tilman (1990) showed that two years of different grass monocultures developed under a common initial soil promoted 10-fold changes in soil nitrogen mineralization mainly driven by belowground biomass and quality which, in turn, was not clearly related to aboveground litter quality. Moretto et al. (2001) found that palatable and non-palatable grasses differed in litter decomposition, and nitrogen and phosphorus release at the leaf, but not at the root level. In a recent meta-analysis of global patterns of root decomposition, Silver and Miya (2001) concluded that the parameters that better explain the variability of root decay rate are not climatic, as in aboveground litter decay models, but litter quality traits, such as calcium, nitrogen, and lignin contents. Several of our findings supported this claim: first, we did not find a correlation between aboveground and neither root litter

quality nor soil nitrogen dynamics. Second, root decomposition and mean annual rainfall of the origin site were not correlated. Third, lignin to nitrogen content explained a significant variability of decomposition rate in roots whereas it did not explain variability in aboveground litter decay patterns. Fourth, the wider differences in litter quality and decomposability were not found among sites or grazing response groups, but between the aboveground and belowground portions of single species. Finally, we found that the effects of grazing on litter quality were frequently reversed depending on whether the aboveground litter or root was under analysis.

In contrast to the pattern observed in roots, the decay rate of aboveground litter was not correlated with its initial lignin content and lignin to nitrogen ratio. The relatively low decomposition rate of forbs from the wet site (particularly *Mentha pulegium*), in spite of their lower lignin to nitrogen ratios, suggest that other secondary compounds such as crude phenolics would have explained a significant part of the variability in decomposition. Although we did not measure them in this study, previous work and the obvious observation that *M. pulegium* is a strongly aromatic herb indicate that these forbs have high levels of these compounds (Semmartin et al. 1999). Findlay et al. (1996) arrived to similar conclusions when they found that cotton leaf decomposition was not correlated with leaf nitrogen content but with phenolics content. Moreover, Grime et al. (1996) showed that other leaf traits, that may be summarized assessing the level of consumption by a generalist herbivore, explained 56% of the variability found in the leaf decomposition rate of a broad range of species, which raises the complexity of the process. A possible explanation for our dissimilar level of correlation of aboveground litter and roots is that, as found in pine needles, lignin only played a significant role in decomposition in later stages, when lignin concentration is about 10–20% (Johansson et al. 1995). In our data-set, roots had the greatest lignin concentration, and similar to pine needle values.

It is commonly accepted that herbivores exert a positive effect on nutrient cycling (Wedin 1994). There is a number of studies who have found a stimulating effect of grazing on nutrient cycling at different scales, some of them without addressing any particular mechanism (Frank and Evans 1997, McNaughton et al. 1997, Frank and Groffman 1998), while some others testing one or several specific hypotheses (reviewed by Bardgett et al. 1998). Some studies, however, found results that suggest that grazing retards nutrient cycling through a variety of mechanisms (Ritchie et al. 1998, Moretto et al. 2001). We believe that any integrative model aimed at disentangle plant–herbivore interactions at the ecosystem level should take into account these mechanisms within the context of the groups of species

that are diminished and promoted by grazing. As Bardgett et al. (1998) stressed, the empirical evidence of the consequences of shifts in species composition on nutrient cycling mediated by herbivores is scarce. We were interested in isolating the species effects on nutrient cycling, and we are aware of the limited extrapolation of greenhouse approaches, since they do not necessarily mimic the field conditions. However, recent field evidence documented a similar pattern in natural conditions (Moretto et al. 2001, Golluscio 2002). Nevertheless, it can be argued that our approach has also strengths in relation to field experiments in which manipulation of environmental noise to isolate treatment effects can be very difficult. Our data, which unequivocally assayed the potential grazing induced effects on litter quality and nutrient cycling, provides evidence that when coupled with the vast knowledge about the effects of grazing on plant community structure, is relevant in order to weigh the relative importance of the different mechanisms involved in plant–herbivore interactions. Further, finding global patterns related to groups of plants replaced as well as the global patterns of root to shoot ratios associated with climate and species replacements, and their impacts on nutrient cycling might allow us, using relatively simple variables, to know whether or not this mechanism is relevant to improve predictions of the final effect of herbivores on nutrient availability in an ecosystem level approach.

**Acknowledgements** – We thank Sebastián Aguiar, Lucas Garibaldi, and Mario Tagliacuzzi for help with experiment assembly and samples processing. Nilda Diddoné helped us with the lignin and fiber analyses. The owners of “Las Chilcas” farm kindly allowed us to sample on their property. Martín Oesterheld contributed with valuable insight on several aspects of this manuscript. Agustín Grimoldi and Enrique Chaneton made helpful comments during different stages of this study. This study was supported by grants of ANCyT (Picts 99: 6761 and 6641), and Universidad de Buenos Aires (JG14). MS was supported by Fundación Antorchas and Fundación René Baron doctoral fellowship and by a CONICET postdoctoral fellowship.

## References

- Aber, J. D. and Melillo, J. M. 1991. Terrestrial ecosystems. – Saunders College Publishing.
- Aguiar, M. R., Cipriotti, P. A., Batista, W. B. et al. 1999. Viabilidad de poblaciones de gramíneas patagónicas en peligro de extinción por sobrepastoreo. I. Estructura de poblaciones. – XIX Reunión Argentina de Ecología, Asociación Argentina de Ecología, pp. 220.
- Austin, A. T. and Vitousek, P. M. 2000. Precipitation, decomposition and litter decomposability of *Metrosideros polymorpha* in native forests on Hawaii. – J. Ecol. 88: 129–138.
- Bardgett, R., Wardle, D. and Yeates, G. 1998. Linking above-ground and below ground interactions: how plant responses to foliar herbivory influence soil organisms. – Soil Biol. Biochem. 30: 1867–1878.

- Bóo, R. M., Lindstrom, L. I., Elia, O. R. et al. 1993. Botanical composition and seasonal trends of cattle diet in central Argentina. – *J. Range Manage.* 46: 479–482.
- Breman, H. and de Wit, C. 1983. Rangeland productivity and exploitation in the Sahel. – *Science* 221: 1341–1347.
- Burke, I. C., Lauenroth, W. K. and Parton, W. J. 1997. Regional and temporal variation in net primary production and nitrogen mineralization in grasslands. – *Ecology* 78: 1330–1340.
- Cabrera, A. 1976. Regiones fitogeográficas argentinas. – In: *Enciclopedia Argentina de Agricultura y Jardinería*, Tomo II, Fascículo 2, Acmé.
- Cano, E. 1975. Pastizales en la región central de la provincia de La Pampa. – *IDIA* 3: 1–15.
- Chaneton, E. J., Lemcoff, J. H. and Lavado, R. S. 1996. Nitrogen and phosphorus cycling in grazed and ungrazed plots in a temperate subhumid grassland in Argentina. – *J. Appl. Ecol.* 33: 291–302.
- Chaneton, E. J., Perelman, S. B., Omacini, M. et al. 2002. Grazing, environmental heterogeneity and alien plant invasions in temperate grasslands. – *Biol. Invasions* 4: 7–24.
- Cornelissen, J. H. C. 1996. An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types. – *J. Ecol.* 84: 573–582.
- Coughenour, M. B. 1985. Graminoid responses to grazing by large herbivores: adaptations, exaptations and interacting processes. – *Ann. Miss. Bot. Gard.* 72: 852–863.
- Coupland, R. 1992. Overview of the grasslands of North America. – In: Coupland, R. (ed.), *Natural Grasslands. Introduction and Western hemisphere*. Elsevier, pp. 147–150.
- Díaz, S. and Cabido, M. 2001. Vive la différence: plant functional diversity matters to ecosystem processes. – *Trends Ecol. Evol.* 16: 646–655.
- Distel, R. A. and Bóo, R. M. 1996. Vegetation states and transitions in temperate semiarid rangelands of Argentina. – *Proc. Fifth Int. Rangeland Congr., Soc. Range Manage.*, pp. 117–118.
- Enríquez, S., Duarte, C. M. and Sand-Jensen, K. 1993. Patterns in decomposition rates among photosynthetic organisms: the importance of detritus C: N: P content. – *Oecologia* 94: 457–471.
- Fahnestock, J. T. and Detling, J. K. 2002. Bison–prairie dog–plant interactions in a North American mixed-grass prairie. – *Oecologia* 132: 86–95.
- Findlay, S., Carreiro, M., Kriskich, V. et al. 1996. Effects of damage to living plants on leaf litter quality. – *Ecol. Appl.* 6: 269–275.
- Frank, D. and Evans, E. 1997. Effects of native grazers on grassland N cycling in Yellowstone National Park. – *Ecology* 78: 2238–2248.
- Frank, D. and Groffman, P. 1998. Ungulate vs landscape control of soil C and N processes in grasslands of Yellowstone National Park. – *Ecology* 79: 2229–2241.
- Golluscio, R. A. 2002. El conflicto entre la limitación por agua y por nitrógeno como determinante de las estrategias de las plantas de zonas áridas. – PhD thesis, Univ. of Buenos Aires.
- Golluscio, R. A., León, R. J. C. and Perelman, S. B. 1982. Caracterización fitosociológica de la estepa del oeste de Chubut, su relación con el gradiente ambiental. – *Boletín de la Sociedad Argentina de Botánica* 21: 229–324.
- Grime, J. P., Cornelissen, H. C., Thompson, K. et al. 1996. Evidence of a causal connection between anti-herbivore defence and the decomposition rate of leaves. – *Oikos* 77: 489–494.
- Grime, J. P., Thompson, K., Hunt, R. et al. 1997. Integrated screening validates primary axes of specialization in plants. – *Oikos* 79: 259–281.
- Hobbie, S. E. 1992. Effects of plants species on nutrient cycling. – *Trends Ecol. Evol.* 7: 336–339.
- Hobbie, S. E. 1996. Temperature and plant species control over litter decomposition in Alaskan tundra. – *Ecol. Monogr.* 66: 503–522.
- Holland, E. A., Parton, W. J., Detling, W. K. et al. 1992. Physiological responses of plant populations to herbivory and their consequences for ecosystem nutrient flow. – *Am. Nat.* 140: 685–706.
- Jackson, R. B., Canadell, J., Ehleringer, J. R. et al. 1996. A global analysis of root distributions for terrestrial biomes. – *Oecologia* 108: 389–411.
- Johansson, M. B., Berg, B. and Meentemeyer, V. 1995. Litter mass-loss rates in late stages of decomposition in a climatic transect of pine forests. Long-term decomposition in a Scots pine forest. – *Can. J. Bot.* 73: 1509–1521.
- León, R. J. C., Bran, D., Collantes, M. B. et al. 1998. Grandes unidades de vegetación de la Patagonia extra andina. – *Ecol. Austral* 8: 125–144.
- Llorens, E. M. 1995. Viewpoint: the state and transition model applied to the herbaceous layer of Argentina's calden forest. – *J. Range Manage.* 48: 442–447.
- McNaughton, S. 1983. Serengeti grassland ecology: the role of composite environmental factors and contingency in community organization. – *Ecol. Monogr.* 53: 291–320.
- McNaughton, S. J., Oesterheld, M., Frank, D. et al. 1989. Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. – *Nature* 341: 142–144.
- McNaughton, S. J., Banyikwa, F. F. and McNaughton, M. M. 1997. Promotion of the cycling of diet-enhancing nutrients by African grazers. – *Science* 278: 1798–1800.
- Melillo, J. M., Aber, J. D. and Muratore, J. F. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. – *Ecology* 63: 621–626.
- Milchunas, D. G. and Lauenroth, W. K. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. – *Ecol. Monogr.* 63: 327–366.
- Milchunas, D. G., Sala, O. E. and Lauenroth, W. K. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. – *Am. Nat.* 132: 87–106.
- Moretto, A. S., Distel, R. A. and Diddoné, N. G. 2001. Decomposition and nutrient dynamic of leaf litter and roots from palatable and unpalatable grasses in a semi-arid grassland. – *Appl. Soil Ecol.* 18: 31–37.
- Murphy, K. L., Burke, I. C., Vinton, M. A. et al. 2002. Regional analysis of litter quality in the central grassland region of North America. – *J. Veg. Sci.* 13: 395–402.
- Oesterheld, M., McNaughton, S. J. and Sala, O. E. 1992. Effect of animal husbandry on herbivore-carrying capacity at a regional scale. – *Nature* 356: 234–236.
- Oesterheld, M., Loreti, J., Semmartin, M. et al. 1999. Grazing, fire and climate effects on primary productivity of grasslands and savannas. – In: Walker, L. (ed.), *Ecosystems of disturbed ground*. Elsevier, pp. 287–306.
- Olofsson, J. and Oksanen, L. 2002. Role of litter decomposition for the increased primary production in areas heavily grazed by reindeer: a litterbag experiment. – *Oikos* 96: 507–515.
- Olson, J. S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. – *Ecology* 44: 322–331.
- Parton, W. J., Schimel, D. S., Cole, C. V. et al. 1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. – *Soil Sci. Soc. Am. J.* 51: 1173–1179.
- Paruelo, J. M., Aguiar, M. R. and Golluscio, R. A. 1988. Soil water availability in the Patagonian arid steppe: gravel content effect. – *Arid Soil Res. Rehab.* 2: 67–74.
- Pastor, J., Dewey, B., Naiman, R. et al. 1993. Moose browsing and soil fertility in the boreal forest of Isle Royale national park. – *Ecology* 74: 467–480.
- Perelman, S. B., León, R. J. C. and Bussacca, J. P. 1997. Floristic changes related to grazing intensity in a Patagonian shrub steppe. – *Ecography* 20: 400–406.

- Perelman, S. B., León, R. J. C. and Oesterheld, M. 2001. Cross-scale vegetation patterns of Flooding Pampa grasslands. – *J. Ecol.* 89: 562–577.
- Pisani, J. M., Distel, R. A. and Bontti, E. E. 2000. Diet selection by goats on a semi-arid shrubland in central Argentina. – *Ecol. Austral* 10: 103–108.
- Ritchie, M. E., Tilman, D. and Knops, J. M. H. 1998. Herbivore effects on plant and nitrogen dynamics in oak savanna. – *Ecology* 79: 165–177.
- Sala, O., Deregibus, V., Schlichter, T. et al. 1981. Productivity dynamics of a native temperate grassland in Argentina. – *J. Range Manage.* 34: 48–51.
- Sala, O. E., Oesterheld, M., León, R. J. C. et al. 1986. Grazing effects upon plant community structure in subhumid grasslands of Argentina. – *Vegetatio* 67: 27–32.
- Sala, O. E., Parton, W. J., Joyce, L. A. et al. 1988. Primary production of the central grassland region of the United States. – *Ecology* 69: 40–45.
- Semmartin, M., Oesterheld, M. and Ghersa, C. M. 1999. Análisis de compuestos secundarios en especies de un pastizal de la Pampa Deprimida. – XIX Reunión Argentina de Ecología. Asociación Argentina de Ecología, p. 159.
- Silver, W. L. and Miya, R. K. 2001. Global patterns in root decomposition: comparisons of climate and litter quality effects. – *Oecologia* 129: 407–419.
- Sims, P. L. and Singh, J. S. 1978. The structure and function of ten western North American grasslands. III. Net primary production, turnover and efficiencies of energy capture and water use. – *J. Ecol.* 66: 573–597.
- Soriano, A. 1983. Deserts and semi-deserts of Patagonia. – In: West, N. (ed.), *Temperate deserts and semi-deserts*. Elsevier, pp. 423–460.
- Soriano, A. 1992. Río de la Plata Grasslands. – In: Coupland, R. (ed.), *Ecosystems of the World. Natural Grasslands. Introduction and Western Hemisphere*. Elsevier, pp. 367–407.
- Soriano, A., Sala, O. E. and Perelman, S. B. 1994. Patch structure and dynamics in a Patagonian arid steppe. – *Vegetatio* 111: 127–135.
- Swift, M., Heal, O. and Anderson, J. 1979. *Decomposition in terrestrial ecosystems*. – Blackwell Scientific Publications.
- Van Soest, P. J. and Wine, R. H. 1968. The determination of lignin and cellulose in acid detergent fiber with permanganate. – *J. Assoc. Offic. Anal. Chem.* 51: 780–787.
- Vinton, M. A. and Burke, I. C. 1995. Interactions between individual plant species and soil nutrient status in shortgrass steppe. – *Ecology* 76: 1116–1133.
- Wardle, D. A., Bonner, K. I. and Nicholson, K. S. 1997. Biodiversity and plant litter: experimental evidence which does not support the view that enhanced species richness improves ecosystem function. – *Oikos* 79: 247–258.
- Wedin, D. A. 1994. Species, nitrogen and grassland dynamics: the constraints of stuff. – In: Jones, C. and Lawton, J. H. (eds), *Linking species and ecosystems*. Chapman and Hall, pp. 253–262.
- Wedin, D. A. and Tilman, D. 1990. Species effects on nitrogen cycling: a test with perennial grasses. – *Oecologia* 84: 433–441.
- Wieder, R. and Lang, G. 1982. A critique of the analytical methods used in examining decomposition data obtained from litter bags. – *Ecology* 63: 1636–1642.
- Zar, J. H. 1999. *Biostatistical analysis*, 4th ed. – Prentice Hall.