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REGULAR ARTICLE

Grazing history effects on above- and below-ground litter decomposition and nutrient cycling in two co-occurring grasses

María Semmartin · Lucas A. Garibaldi · Enrique J. Chaneton

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Abstract Large herbivores may alter carbon and nutrient cycling in soil by changing above- and below-ground litter decomposition dynamics. Grazing effects may reflect changes in plant allocation patterns, and thus litter quality, or the site conditions for decomposition, but the relative roles of these broad mechanisms have rarely been tested. We examined plant and soil mediated effects of grazing history on litter mass loss and nutrient release in two grazing-tolerant grasses, *Lolium multiflorum* and *Paspalum dilatatum*, in a humid pampa grassland, Argentina. Shoot and root litters produced in a common garden by conspecific plants collected from grazed and ungrazed sites were incubated under both grazing conditions. We found that grazing history effects on litter decomposition were stronger for shoot than for root material. Root mass loss was neither affected by litter origin nor incubation site, although roots from the grazed origin immobilised more nutrients. Plants from the grazed site produced shoots with higher cell soluble contents and lower lignin:N ratios. Grazing effects mediated by shoot litter origin depended on the species, and were less apparent than incubation site effects. *Lolium* shoots from the grazed site decomposed and released nutrients faster, whereas *Paspalum* shoots from the grazed site retained more nutrient than their respective counterparts from the ungrazed site. Such divergent, species-specific dynamics did not translate into consistent differences in soil mineral N beneath decomposing litters. Indeed, shoot mass loss and nutrient release were generally faster in the grazed grassland, where soil N availability was higher. Our results show that grazing influenced nutrient cycling by modifying litter breakdown within species as well as the soil environment for decomposition. They also indicate that grazing effects on decomposition are likely to involve aerial litter pools rather than the more recalcitrant root compartment.

Keywords Flooding Pampa · Grassland · Herbivory · Nitrogen · Phosphorus · Roots

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Introduction

Large herbivores act as major drivers of terrestrial biogeochemical cycles, as they regulate carbon and nutrient fluxes linking the producer and decomposer subsystems (McNaughton et al. 1997; De Mazancourt et al. 1998; Bardgett and Wardle 2003). In particular, herbivory may influence organic matter decomposition and nutrient cycling rates by changing the quality of plant litter entering the soil through both above and belowground pathways (Holland and Detling 1990; Pastor et al. 1993; Bardgett et al. 1998; Olofsson and Oksanen 2002; Wardle et al. 2002). Moreover, prior grazing history may either accelerate or retard nutrient release from litter by altering the soil environment for decomposition (Shariff et al. 1994; Bardgett et al. 1998; Sankaran and Augustine 2004). While grazing effects on decomposition have been shown in a number of studies, few have examined the relative roles of litter quality and site conditions as intermediary factors (Olofsson and Oksanen 2002; Garibaldi et al. 2007), and how they might differentially involve aerial and root fractions of grazing-tolerant species.

Grazing effects on decomposition can be mediated by physiological changes at the whole-plant level that in turn influence the quality of litter returned to soil by grazing-tolerant species (Holland et al. 1992; Bardgett and Wardle 2003). Herbivores may drastically change patterns of energy and nutrient allocation in plants (Jaramillo and Detling 1988; Dyer et al. 1991). Plant regrowth following defoliation often increases nutrient concentrations in aerial tissues, which may thus enhance subsequent decomposition rates of senescent shoots (Ruess and McNaughton 1987; Holland et al. 1992). Grazing also affects root tissue chemistry through changes in carbon allocation and nutrient uptake (McNaughton and Chapin 1985; Jaramillo and Detling 1988; Holland and Detling 1990), having potentially variable effects on root litter breakdown (Bardgett et al. 1998; Semmartin et al. 2004). It has been suggested for certain plant species that grazing may favour morphotypes with highly decomposable litter that releases nutrients rapidly during decomposition (Holland et al. 1992; Olofsson and Osksanen 2002; Semmartin and Ghersa 2006). High herbivory pressure could alternatively promote grazing-resistant genotypes carrying traits such as low shoot N contents or greater allocation to roots (Coughenour et al. 1985; Dyer et al. 1991; Painter et al. 1993), which may eventually retard decomposition and nutrient mineralisation (Pastor and Cohen 1997). Intraspecific genetic differences associated with plant resistance to invertebrate herbivory have also been found to influence leaf-litter decomposition rates in old fields (Uriarte 2000) and woodlands (Madritch and Hunter 2002; Schweitzer et al. 2005). Noticeably, however, whereas grazing-induced effects on aerial litter quality and decomposition have been addressed by several studies (Bardgett and Wardle 2003; Garibaldi et al. 2007), analogous functional changes in root litter have rarely been considered (Moretto et al. 2001). In grassland ecosystems, a major fraction of plant carbon and nutrients transferred to soil go through the belowground pathway (Parton et al. 1988; Chaneton et al. 1996; Piñeiro et al. 2006). Despite the prominent role of root turnover in grassland biogeochemistry, little is known about the magnitude and direction of grazing effects on belowground litter decomposition as compared to those induced through aerial litter.

Large herbivores may additionally affect nutrient cycling by altering the soil biotic and abiotic conditions for decomposition (Shariff et al. 1994; Bardgett et al. 1998). Dung and urine deposition by grazing animals exert a powerful influence on soil nutrient pools and microbial communities (Seagle and McNaughton 1992; Bardgett et al. 2001; Sankaran and Augustine 2004). As a result, grazers have been found to enhance soil nitrogen availability and litter breakdown (Shariff et al. 1994; McNaughton et al. 1997; Tracy and Frank 1998; Olofsson and Oksanen 2002), with concomitant shifts in functional composition of the soil biota (Bardgett et al. 2001; Grayston et al. 2004). Long-term grazing may select for soil decomposers adapted to degrade litter from grazing-tolerant species leading to positive plant-soil feedbacks in nutrient cycling (Bardgett and Wardle 2003). On the other hand, plant biomass removal and soil trampling associated with heavy grazing may alter soil properties such as bulk density, moisture and salinity contents (Lavado and Taboada 1988), while decreasing microbial community biomass (Sankaran and Augustine 2004), to the extent that may negatively impact on decomposition rates. However, few studies have been designed to untangling changes in nutrient cycling driven by the imprint of prior grazing history on soil conditions for decomposition and by whole-plant shifts in the quality of litter inputs to soil (cf. Schweitzer et al. 2005).

We examined plant and soil mediated effects of grazing history on litter decomposition and nutrient turnover in two grazing-tolerant grass species. Shoot and root litter produced under common garden conditions by *Lolium multiflorum* Lam. and *Paspalum dilatatum* Poir. plants collected from long-term grazed and ungrazed sites were incubated at both grazing conditions in a Flooding Pampa grassland, Argentina. By reciprocally incubating the litter shed by conspecifics from grazed and ungrazed areas, we were able to decouple effects of prior grazing driven by litter functional attributes from those associated with the decomposition environment. Furthermore, we homogenised canopy-related differences between grazed and ungrazed areas by removing all aerial vegetation, which allowed us to focus on soil mediated effects of grazing history on litter breakdown. We specifically asked (1) how litter origin and incubation site, singly or interactively, influence litter decomposition of two co-occurring grasses, and (2) whether grazing history affects decomposition dynamics in a consistent way for shoot and root litter substrates.

Materials and methods

Study area and plant species

We conducted litterbag experiments in two adjacent grazed and ungrazed sites located on a natural grassland at the centre of the Flooding Pampas in eastern Argentina (36° 30′ S, 58° 30′ W). The area has a mean annual precipitation of ~960 mm and a mean annual temperature of 14.9°C; monthly temperatures vary from 8°C in July to 22°C in January. The landscape is extremely flat; soils are Typic Natraquols with a loamy A horizon (pH=6.7), 3.5% organic carbon, and 0.28% total nitrogen (Lavado and Taboada 1988; Chaneton and Lavado 1996). Flooding events occur almost annually during periods of heavy rainfall and may last for several weeks (Lavado and Taboada 1988). The local vegetation corresponds to a humid mesophytic grassland, the most widespread community type in the region (Perelman et al. 2001). The study area had been managed for cattle grazing at moderate stocking rates (~0.6 cow ha^{-1} yr^{-1}) for at least 50 years.

In this system, grazing exerts a major impact on grassland community structure (Soriano 1992; Rusch and Oesterheld 1997; Chaneton et al. 2002). Grazed communities may comprise up to 25 species/m^2 (total richness ~60 spp), while cattle exclusion decreases plant richness by almost 30% (Chaneton et al. 2002; Semmartin et al. 2007). Grazing strongly alters energy and nutrient flows between vegetation and soil compartments (Doll 1991; Chaneton et al. 1996; Piñeiro et al. 2006). Nutrient budgets for grazed and ungrazed areas indicated that cattle grazing accelerates N and P cycling during the main growing season (Chaneton et al. 1996), which may be partly explained by grazing-induced changes in plant community composition (Semmartin et al. 2004; Garibaldi et al. 2007). Long-term cattle exclusion has shown that several grazing-tolerant grasses contribute substantially to community biomass both in grazed and ungrazed areas (Facelli 1988; Rusch and Oesterheld 1997). How these ubiquitous plant species respond to grazing history in terms of their litter functional attributes and likely influence on decomposition dynamics is virtually unknown (Semmartin and Ghersa 2006).

We focused on two grass species, *L. multiflorum* and *P. dilatatum* (hereafter named only by genus), which are highly palatable to cattle but maintain large viable populations in chronically grazed paddocks as well as in long-term ungrazed areas (Deregibus et al. 1994; Rusch and Oesterheld 1997). *Lolium* is a naturalised, C_3 annual bunchgrass attaining its maximum biomass in late spring; *Paspalum* is a native, C_4 perennial rhizomatous grass, with its peak biomass in summer. Both species exhibit substantial shoot plasticity and regrowth ability upon defoliation (Casal et al. 1987; Gibson et al. 1992; Loreti et al. 2001). *Lolium* populations regenerate every autumn from transient soil seed banks (Deregibus et al. 1994). *Paspalum* persists mainly through asexual growth of established ramets and relies on architectural plasticity for avoiding herbivory (Loreti et al. 2001). In the study area, *Lolium* accounts for about 8 and 48% of the total plant cover in grazed and ungrazed plots, respectively, while *Paspalum* represents about 3% of the cover in both grazing conditions (Facelli 1988; Rusch and Oesterheld 1997; Semmartin et al. 2007).

Litter collection and experimental design

During July–September 2001 (mid winter–early spring), plants of both species were taken from two adjacent sites differing in grazing history. One site was grazed year-round at the nominal stocking rate, while the other was a 18 year-old, 4-ha exclosure protected from cattle

grazing (hereafter 'grazed' and 'ungrazed' sites, respectively). Ten individuals of each species were dug out with a 30 cm-deep soil core from the rooting zone and were transplanted to a common garden at the College of Agronomy campus in Buenos Aires, Argentina. Plants were grown in outdoor containers and watered as needed. After 3 weeks of acclimation, we proceeded to harvest all senescent aboveground material (leaves + stems, hereafter 'shoots') shed by the plants over a five-month period. A mix of living and dead root material (hereafter 'roots') was also collected during a final, destructive harvest. By using litter derived from plants grown under common conditions we reduced, but may have not fully eliminated, short-term effects on litter quality associated with recent grazing events. The litter material was washed, air-dried, cut into 2 cm-long pieces and pooled according to species, tissue type and plant origin (grazed vs. ungrazed grassland). Litter bags (6 cm×10 cm) were made of 0.35 mm-mesh nylon screen and filled with 1 g of air-dried litter.

Between 15 February and 9 July 2002 (mid summer through mid winter), we conducted parallel litterbag experiments at the two same sites from which the original plants had been collected. The grazed site was fenced for the duration of the experiment. In each site, the design comprised 8 litter substrates, resulting from 2 species (*Lolium* and *Paspalum*) × 2 tissue types (shoots and roots) × 2 origins (grazed and ungrazed), plus a control bag filled with plastic 'litter' (see below). Litterbags were collected after 45, 90 and 160 days of incubation, with five replicates per harvest date, for a total of 120 litterbags (plus five plastic controls) per incubation site. Within each site, litterbags were randomly distributed on a 36 m^2 grid. Shoot litterbags were placed onto the soil surface, while root litterbags were buried 2 cm deep, horizontally, and covered with soil. Bags filled with plastic (non decomposable) 'litter' were included to test for inter-site differences in soil N availability in the absence of plant litter effects. To prevent root ingrowth, each bag was enclosed by a 15 cm-diameter× 20 cm-long PVC core sunk 18 cm deep; these cores were hand-weeded periodically. Three extra litterbags per substrate type were treated as described above, but were immediately retrieved to the laboratory and their dry weight used to adjust the initial litter mass for eventual manipulation losses. This material was also used for analyses of initial litter chemistry.

Two months before the experiment, all aerial vegetation was removed from each grid using a systemic herbicide (glyphosate, 0.6 g/m^2). Glyphosate effects on soil properties are usually negligible but may slightly stimulate soil microbial activity (Busse et al. 2001). Residual effects may be discarded since glyphosate undergoes rapid degradation or immobilisation in clayed soils (Busse et al. 2001; Araújo et al. 2003). This pre-treatment homogenised the grazed and ungrazed sites with regard to canopy-related microclimate conditions relevant to decomposition. Total rainfall during the experiment was 744 mm (66% above a 45-year average). As a result, the study area became flooded in the end of March 2002 and remained so until the end of the experiment. The grazed and ungrazed sites were similarly waterlogged with 3–10 cm standing water. Flooding alters soil nutrient dynamics (Ponnamperuma 1984) and therefore our findings should be interpreted with this environmental setting in mind.

Litter and soil analyses

After each harvest, litter was carefully brushed, washed, air-dried to constant weight, and weighed to determine the mass remaining. Nitrogen (N), phosphorus (P), cell solubles, celluloses (cellulose + hemicellulose) and lignin concentrations, and the lignin:N ratio, were determined to characterise initial 'quality' for each litter type. Nutrient concentrations were also determined for the litter remaining in each harvest date. Litter N and P concentrations were obtained using standard Kjeldahl acid digestions and were colorimetrically assayed in an Alpkem (Wilsonville, OR, USA) autoanalyzer. Fibre determinations followed the Van Soest et al. (1991) procedure. Changes in litter N and P contents were calculated by multiplying the remnant litter mass by the corresponding nutrient concentrations; data were expressed as percentages of the initial N and P contents. Soil N availability was measured beneath each litterbag (2 cm depth) after 45 days of incubation. Since the study area became flooded in late March (~day 40), measurements were discontinued thereafter. Soil mineral N was extracted with a 2 mol/L KCl solution and colorimetrically assayed for ammonium and nitrate concentrations (Alpkem autoanalyser).

Data analysis

Overall differences in initial litter chemistry were examined using multivariate analysis of variance

(MANOVA) testing for effects of tissue type, species and origin of litter, followed by univariate ANOVAs performed on each dependent variable. Changes in litter mass remaining and in litter N and P content during decomposition were examined through four-way ANOVAs. Since shoot and root litterbags were placed in different positions, absolute differences between above- and belowground litter decomposition may not be strictly comparable (Gholz et al. 2000). Thus, analyses were performed separately for shoot and root substrates, with species, litter origin, incubation site and harvest date as main factors. Although ANOVA models included all higher-order interactions, we focused on interaction terms implying a grazing history effect on decomposition, either through litter origin or incubation site. Soil mineral N was first evaluated by a two-way ANOVA testing for effects of incubation site and harvest date (0 vs. 45 days) on soil N measured beneath control (plastic litter) bags. In addition, differences in soil N availability associated with litter decomposition patterns were examined for shoot and root litters using separate three-way ANOVAs, with species, litter origin and incubation site as main factors. Tukey tests ($P<0.05$) were used for post-hoc multiple comparisons among treatments. Note that in all analyses the incubation site effects were based on one location per grazing condition, meaning that statistical differences between sites cannot be unequivocally attributed to prior grazing management. However, when a significant site effect was found, we relied on the fact that, before grazing was excluded in 1983, the study sites could not be distinguished with regard to plant community, soil type or flooding regime.

Results

Initial litter chemistry

Multivariate ANOVA indicated that tissue type, species and their interaction accounted for most variation in initial litter chemistry (Table 1). Roots generally contained more lignin and had higher lignin:N ratios than shoots (Table 2). *Lolium* litter types had higher nutrient and cell soluble contents, and lower celluloses and lignin:N ratios, than *Paspalum* ones (Tables 1, 2). Litter origin had a relatively small but significant overall effect on litter quality ($P<0.05$, Wilk's lambda). Univariate tests revealed that grazing (origin) effects on individual chemical traits largely depended on tissue type and marginally on the grass species (Table 1). Irrespective of species, plants from the grazed site produced shoots with higher cell solubles content and lower lignin:N ratios than those from the ungrazed site, whereas the opposite pattern was found in roots ($P_{\text{tissue} \times \text{origin}}=0.04$; Table 2). In addition, *Lolium* plants from the grazed site shed litter with a higher N content than conspecifics from the ungrazed site, whereas *Paspalum* litter showed the opposite trend ($P_{\text{species} \times \text{origin}}=0.052$; Table 2).

Litter decomposition

In preliminary analyses including all four experimental factors, shoots decomposed much faster than roots irrespective of species, litter origin and incubation site (four-way ANOVA, $P<0.0001$). After 160 days, litter mass remaining ranged 20–75% and 73–96%, for shoots and roots, respectively (Fig. 1). Hence, we carried out separate analyses for each tissue type. Shoot litter decomposition depended strongly on the species and incubation site (Table 3). *Lolium* shoots decomposed faster than *Paspalum* shoots, and shoots incubated in the grazed site decomposed ~20% faster than those in the ungrazed site (Fig. 1, upper panels). The litter origin further affected patterns of mass loss in shoots but not roots (Table 3). Shoots produced by *Lolium* plants taken from the grazed site decomposed slightly, but significantly, faster than those from the ungrazed site, yet only when incubated in the grazed site. In contrast, no significant effect of grazing origin was detected for *Paspalum* shoots ($P_{\text{species} \times \text{origin} \times \text{site}}=0.015$; Fig. 1). Root mass loss differed between species, with *Lolium* roots decomposing faster than *Paspalum* ones, irrespective of litter origin and incubation site (Table 3; Fig. 1, lower panels).

Nutrient dynamics in litter and soil

Species, origin of litter and incubation site interactively influenced N and P dynamics during litter breakdown (Table 3). *Lolium* shoots released N and P faster than *Paspalum* shoots which, in turn, tended to immobilise both nutrients. This species-specific pattern was most evident for shoot litter shed by plants originary from the grazed site ($P_{\text{species} \times \text{origin}}<0.0005$; Figs. 2, 3). Furthermore, rates of N and P release from decomposing shoots were faster in the grazed site ($P_{\text{site} \times \text{harvest}}=$

Table 1 MANOVA (Wilk's λ) and ANOVA (*F* values) results for the initial chemistry of *Lolium* and *Paspalum* litter types

Source	MANOVA	Univariate ANOVAs					
	Wilk's λ	Nitrogen	Phosphorus	Solubles	Celluloses	Lignin	Lignin:N
Tissue	0.20***	5.64**	0.83	17.7***	0.08	14.8***	9.56**
Species	0.15***	29.1****	10.94***	22.2***	8.16***	2.82	12.9***
Origin	**0.33****	0.61	2.12	**3.31***	0.04	0.96	0.02
Tissue × Species	0.27**	5.61**	0.77	1.3	0.05	0.92	6.88**
Species × Origin	0.52	**4.42***	0.06	0.04	0.93	0.05	1.66
Tissue × Origin	**0.43***	1.18	0.06	**12.41*****	0.24	1.36	**4.82****
Tissue × Species × Origin	0.57	0.71	2.28	0.33	0.10	0.97	0.81

****$P<0.001$,***$P<0.01$, **$P<0.05$, *$P<0.10$

For all effects, degrees of freedom were 5 and 12 (multivariate test), and 1 and 16 (univariate tests). Effects associated with litter origin (i.e., litter produced by plants from grazed vs. ungrazed sites) are shown in bold.

0.0002), where interspecific differences increased significantly over time ($P_{species \times site \times harvest}<0.005$; Figs. 2, 3). Root nutrient dynamics did not differ between incubation sites and mostly reflected litter species × origin interactions, which depended on the nutrient considered (Table 3). In general, N was retained by decomposing roots but this effect was greater for *Paspalum* roots from the grazed origin. In contrast, P tended to be released from roots, although it was retained by *Lolium* roots from the grazed origin (Figs. 2, 3).

Soil N availability beneath control (plastic litter) bags at 0 and 45 days of incubation was, on average, higher in the grazed than in the ungrazed site (41.5 *vs.* 12.2 μg N g^{-1} soil, respectively; $F_{1, 26}=12.8$, $P=0.0014$) and did not differ between dates ($P_{date}=0.30$; $P_{site \times date}=0.35$). The same pattern was found after 45 days of incubation for soil mineral N measured beneath plant litter bags (three-way ANOVA, site effect: shoots, $F_{1, 32}=30.7$, $P<0.0001$; roots, $F_{1, 32}=31.1$, $P<0.0001$; Fig. 4). In addition, soil N levels beneath litterbags were affected by a weakly significant, species × origin × site interaction (shoots, $F_{1, 32}=4.7$, $P=0.038$; roots, $F_{1, 32}=4.22$, $P=0.048$; all other effects $P>0.10$). This likely reflected idiosyncratic differences among microsites amended with either *Lolium* or *Paspalum* litter substrates. Yet, no consistent effects of shoot or root litter origin were detected on soil N levels in grazed or ungrazed grassland ($P>0.05$, Tukey tests; Fig. 4).

Discussion

Large grazers have been shown to influence nutrient cycling through their effects on the quality of litter produced by grazing-tolerant species and the site conditions for decomposition (Holland et al. 1992; Bardgett et al. 1998; Sankaran and Augustine 2004). Yet how these two mechanisms act together affecting above- and belowground litter decomposition within

Table 2 Initial chemical attributes of shoot and root litter produced by *Lolium* and *Paspalum* plants collected from nearby grazed (G) and ungrazed (U) sites in the Flooding Pampa, Argentina

Species	Tissue	Origin	Nitrogen (%)	Phosphorus (%)	Solubles (%)	Cellulose (%)	Lignin (%)	Lignin:N
Lolium	Shoots	U	0.79 (0.06)	0.08 (0.003)	25.5 (1.8)	62.4 (2.1)	9.5 (3.4)	12.7 (4.8)
		G	0.88 (0.16)	0.08 (0.01)	32.5 (1.9)	61.7 (0.4)	5.5 (0.9)	6.4 (0.4)
	Roots	U	1.07 (0.04)	0.10 (0.007)	24.0 (1.2)	64.0 (2.8)	10.6 (0.6)	9.9 (0.8)
		G	1.13 (0.05)	0.08 (0.01)	21.7 (0.3)	59.9 (3.2)	12.5 (2.8)	10.9 (1.9)
Paspalum	Shoots	U	0.69 (0.08)	0.07 (0.001)	19.7 (2.6)	67.5 (5.7)	8.3 (1.9)	12.6 (2.4)
		G	0.64 (0.04)	0.05 (0.008)	24.9 (0.5)	69.5 (0.6)	6.4 (0.1)	10.2 (0.7)
	Roots	U	0.80 (0.07)	0.06 (0.005)	19.6 (2.7)	66.8 (1.9)	14.8 (2.4)	18.7 (3.4)
		G	0.53 (0.02)	0.06 (0.016)	18.0 (0.6)	68.0 (3.2)	13.3 (1.2)	25.5 (3.3)

Data show means, with standard errors in parentheses ($n=3$).

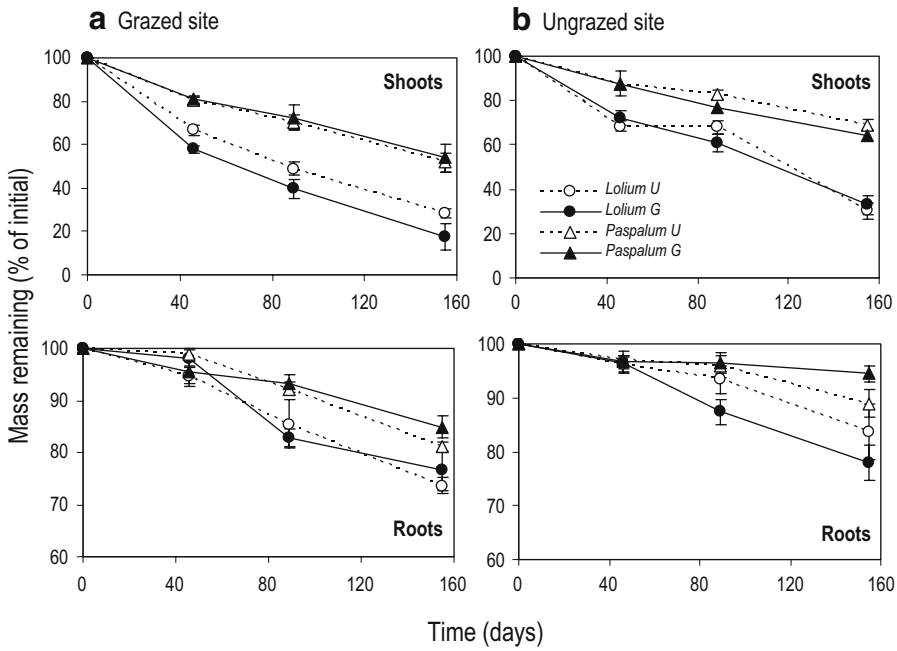

Fig. 1 Changes in litter mass remaining for shoots and roots produced by *Lolium* and *Paspalum* plants from grazed and ungrazed grassland (litter origin), when reciprocally incubated in grazed (**a**) and ungrazed (**b**) sites. Data are means±1 SE (n=5); full statistics are shown in *Table 3*

the same system has remained largely untested. Our results suggest that, in this flood-prone grassland, grazing affected nutrient cycling by changing both the soil environment for decomposition, and the chemical composition and decomposition dynamics of litter derived from two grass species. The latter ('origin') effect indicates that the grazing condition experienced by the plants influenced their subsequent decomposition and nutrient turnover upon tissue senescence. Further, we found that grazing effects on decomposi-

Table 3 ANOVA results (F values) for changes in the litter mass, and nitrogen and phosphorous contents remaining at three harvest dates during decomposition of *Lolium* and *Paspalum* litter substrates incubated in nearby grazed and ungrazed sites

Source	df	Shoot litter			Root litter		
		Mass	Nitrogen	Phosphorus	Mass	Nitrogen	Phosphorus
Species (Sp)	1	256.7***	220.4***	126.3***	18.0***	18.6***	12.7***
Origin (Or)	1	**4.1***	0.9	**19.5*****	0.7	**30.6*****	**14.2*****
Incubation site (Site)	1	**54.9*****	**23.9*****	0.0	2.3	1.5	0.1
Harvest (H)	2	157.5***	46.1***	25.9***	30.6***	32.6***	54.2***
Sp × Or	1	1.7	**12.9*****	**30.7*****	0.1	**26.0*****	**65.4*****
Sp × Site	1	0.7	1.9	**7.3****	0.7	0.6	1.8
Or × Site	1	0.5	0.2	0.2	0.2	0.8	0.2
Sp × H	2	9.0***	17.9***	9.4***	4.6*	0.2	0.7
Or × H	2	0.6	0.5	0.5	1.8	1.1	0.1
Site × H	2	1.7	**9.2*****	**9.2*****	0.8	0.6	0.2
Sp × Or × Site	1	**6.1***	3.7	2.9	0.0	3.8	0.4
Sp × Or × H	2	0.1	1.9	1.2	0.7	0.2	0.6
Sp × Site × H	2	2.8	**10.3*****	**5.5****	1.6	0.4	0.2
Or × Site × H	2	0.8	**3.6***	0.7	0.3	0.1	0.2
Sp × Or × Site × H	2	0.2	0.1	0.1	0.3	1.4	0.1

***P<0.001, **P<0.01, *P<0.05

Litter was produced by plants from grazed or ungrazed grassland ('origin'). Effects associated with grazing history (litter origin and incubation site) are shown in bold. Error term df=96.

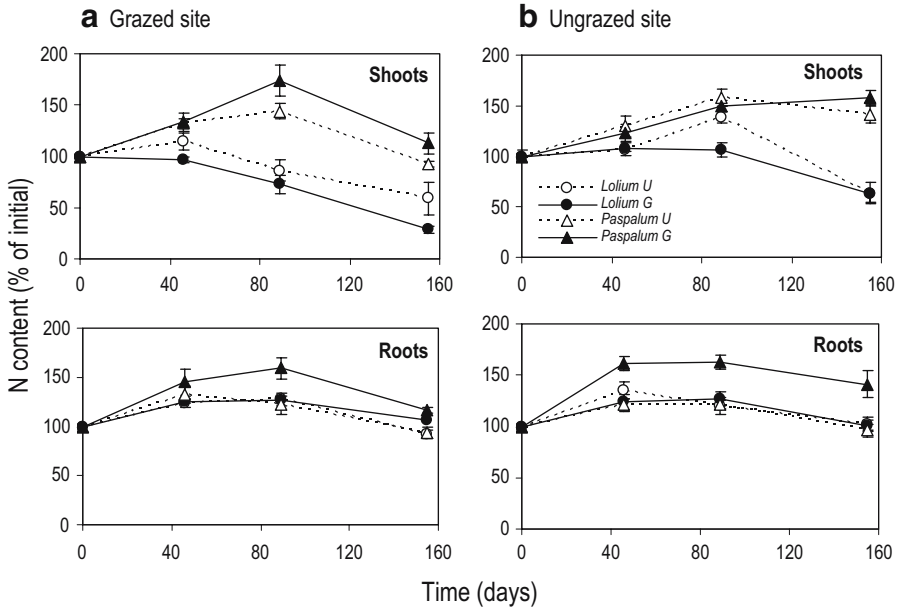

Fig. 2 Nitrogen dynamics in shoot and root litter produced by *Lolium* and *Paspalum* plants from grazed and ungrazed grassland (litter origin), when reciprocally incubated in grazed (**a**) and ungrazed (**b**) sites. Data are means±1 SE (n=5); full statistics are shown in *Table 3*

tion, either plant or soil mediated, mostly involved shoot-derived litter rather than the more recalcitrant, root litter compartment. Whether grazing origin accelerated or retarded shoot decomposition depended on the species. Most importantly, however, shoot decomposition and nutrient release were generally faster in the grazed grassland, which contained higher levels of soil available N than the ungrazed grassland.

In general, grazing effects on decomposition were stronger for shoot than for root litter substrates. Mass loss and nutrient (N, P) release from decomposing shoots were singly or interactively affected by litter origin and incubation site, indicating a role for grazing history in controlling current decomposition processes at the soil surface. In contrast, root decomposition resulted similar in grazed and ungrazed soils, while grazing effects on root N and P turnover mediated by plant origin were inconsistent, as they depended on the nutrient and species considered (Table 3, Figs. 2, 3). The absence of a clear belowground decomposition

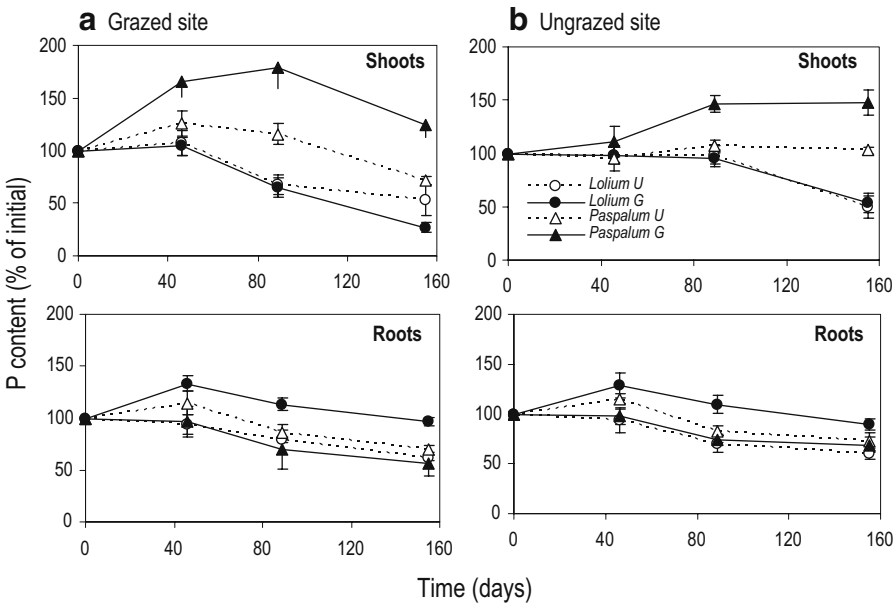

Fig. 3 Phosphorus dynamics in shoot and root litter produced by *Lolium* and *Paspalum* plants from grazed and ungrazed grassland (litter origin), when reciprocally incubated in grazed (**a**) and ungrazed (**b**) sites. Data are means±1 SE (n=5); full statistics are shown in *Table 3*

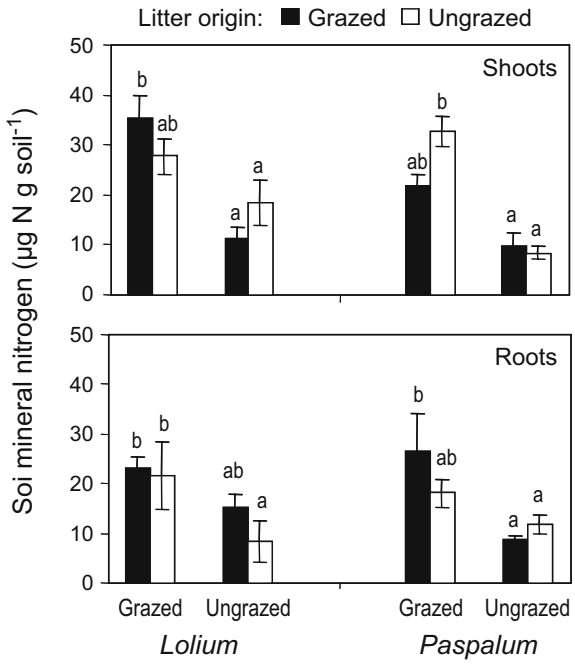

Fig. 4 Soil mineral nitrogen (NH_4^++NO_3^-) beneath shoot (*upper panel*) and root (*lower panel*) litter bags of *Lolium* and *Paspalum* plants from grazed and ungrazed grassland (origin: solid vs. empty bars), decomposing in grazed and ungrazed sites (indicated on the *x* axis). Soil N levels measured after 45 days of litter incubation. Bars show means±1 SE (n=5). Letters above bars indicate significant differences across treatments within panels (P<0.05)

response to grazing coincided with the fact that, overall, root substrates decomposed more slowly than shoots (Biondini and Manske 1996; Gholz et al. 2000; Vivanco and Austin 2006). A comparable pattern was reported by Moretto et al. (2001) for a semiarid grassland. These authors found that shoot litter from palatable grasses decomposed twice as fast as that from unpalatable grasses, although root decomposition rates did not differ between both types of grasses (Moretto et al. 2001). In our study, roots had higher lignin contents and lignin:N ratios than shoots, which could account for their lower decomposibility (Fig. 1). Moreover, relative to shoots, root litter exhibited little variation in initial chemistry in relation to grazing origin (Table 2), a pattern previously found across a range of species from contrasting grassland systems (Semmartin et al. 2004). On the other hand, roots from the grazed site had lower cell solubles and higher lignin:N ratios than plants from the ungrazed site. Although such attributes often correlate negatively with decomposition rates (Silver and Miya 2001; Semmartin et al. 2004), in our case they did not mediate a predictable influence of grazing origin on root decomposition. Alternatively, it might be that the sub-surface soil layer where roots decompose provides a more constant microenvironment that veils the potential influence of litter quality on decomposition (Gholz et al. 2000). It thus appears that grazing history had little impact on belowground litter functioning in the study grasses (cf. Holland and Detling 1990). This finding is mostly relevant to grassland ecosystems, where a major part of the carbon fixed is driven to belowground organs (Piñeiro et al. 2006), and where long-term grazing may have variable impacts on root production (Doll 1991; McNaughton et al. 1998; Frank et al. 2002; Sankaran and Augustine 2004; Semmartin et al. 2007). More work on root litter decomposition across grazing gradients is needed to fully understand the effects of large herbivores on soil carbon and nutrient cycling.

We detected significant grazing effects on shoot litter decomposition associated with plant origin (i.e., whether from grazed or ungrazed grassland), even though the litter we used in the incubations was produced under common growing conditions. This suggests that grazing history shaped, either directly through defoliation or indirectly via changed site conditions, some intrinsic functional traits of these grass species evidenced during the early stages of litter decomposition. Several studies have documented differences in decomposition associated with differences in grazing/browsing resistance *among* plant species (Pastor et al. 1993; Olofsson and Oksanen 2002; Wardle et al. 2002; Garibaldi et al. 2007). In contrast, how grazing modifies decomposition dynamics *within* grazing-tolerant species (Holland et al. 1992; Bardgett et al. 1998) is still not well understood, although both mechanisms may contribute to overall grazing impacts on nutrient cycling (Bardgett and Wardle 2003). It is possible that long-term grazing has selected for certain grass genotypes that are somehow more resistant to defoliation, and also produce a different type of litter with the potential to alter decomposition and nutrient cycling (Holland and Detling 1990). Such indirect effects of plant genotypic variation on ecosystem-level processes have been recently documented for various systems with insect herbivory (Madritch and Hunter 2002; Chapman et al. 2003; Schweitzer et al. 2005).

We found that plants from the grazed site produced litter with lower fibre content (higher cell solubles) and lignin:N ratios than those from the ungrazed site,

which likely contributed to accelerate their decomposition (Aber and Melillo 1991; Vivanco and Austin 2006). Nevertheless, the nature of grazing effects on decomposition through the litter 'origin' depended on the grass species. Whereas *Lolium* shoots from the grazed site had greater N contents, and decomposed and released N faster than their counterparts from the ungrazed site, *Paspalum* shoots from the grazed site showed the opposite trends, retaining more N and P during breakdown. *Lolium* shoots from the grazed site decomposed even faster when incubated in their site of origin, suggesting that grazing induced changes at the whole plant level and in the soil environment that acted synergistically enhancing litter breakdown in this C_3 grass (see also Olofsson and Oksanen 2002). Our results for *Lolium* reinforce previous work conducted at the community level in this grassland (Semmartin et al. 2004; Garibaldi et al. 2007), where grazing-promoted species decomposed more rapidly than grazing-reduced species.

Despite both study grasses being regarded as grazing tolerant species, we observed contrasting, species-specific effects of grazing origin on initial shoot chemistry and nutrient turnover, which amplified intrinsic functional differences between them (Figs. 2, 3). The lack of a consistent response to grazing may seem unsurprising given that the study species differed with regard to life history, growth form and photosynthetic metabolism (see Materials and methods). Yet, how such primary traits might have determined divergent responses to grazing history in terms of litter quality and decomposition is not clear. The limited evidence on this topic suggests that idiosyncratic, intraspecific changes in litter decomposition as a function of prior grazing may be the norm (Ruess and McNaughton 1987; Jaramillo and Detling 1988; Polley and Detling 1988; Holland et al. 1992; Smith 1998; Semmartin et al. 2004). Understanding what traits determine the 'afterlife' plant functional responses to grazing at the within-species level would require comparative analyses using a larger set of litter species, something that has yet to be done for any ecosystem. Interestingly, however, our results for shoot and root substrates show that grazing not only increased differences in decomposition dynamics between species but also between above- and belowground litter pools. Thus, a greater small-scale heterogeneity in nutrient cycling processes may be expected within grazed grasslands.

The aforementioned effects of grazing origin on litter decomposition did not translate into consistent differences in soil N levels beneath litter bags, except for the generally higher soil mineral N measured in shoot than in root amended microsites (Fig. 4). We suggest this result may have partly reflected the influence of soil waterlogging on mineral N pools during the experiment (Ponnamperuma 1984). In particular, flooding conceivably increased denitrification during the summer (Murray et al. 2004; Wrage et al. 2004). Together with the horizontal movement of nutrients dissolved in standing water, gaseous N losses would have contributed to offset any small-scale differences in soil mineral N derived from decomposition of various litter types (see Fig. 4). In addition, under flooding conditions, N being released from decomposing litter may be rapidly taken up by soil microbes close to the soil surface (Ponnamperuma 1984), thus precluding any pattern in soil N availability beneath litterbags. On the other hand, while soil waterlogging may constrain litter decomposition by reducing oxygen supply to microorganisms (Haynes 1986), it is clear from our results (Figs. 1, 2 and 3) that prolonged flooding did not override differences in grass litter dynamics attributable to prior grazing history. In particular, patterns of decomposition documented during the first month of incubation (non-flooded soil) persisted for the remaining of the experiment (flooded soil). Since the study grassland typically undergoes periodical flooding, and litterbags were submerged for most of the experiment, we suggest that our results may be mostly relevant to understand grazing effects on litter breakdown in flood-prone ecosystems.

In this study, the most consistent influence of grazing history on aboveground litter decomposition was associated with the incubation site, and generally implied an acceleration of shoot mass loss and nutrient release. Notice that marked differences in decomposition between grazed and ungrazed sites occurred even though the whole study area remained waterlogged for more than 3 months (see Fig. 4). Because the potential influence of canopy microclimate on soil surface processes was removed, we discard differences in incident radiation, soil temperature and moisture as driving factors (Shariff et al. 1994; Bardgett et al. 1998). If, however, grazed vs. ungrazed sites with intact vegetation had been compared, we suspect that observed differences in litter decomposition might

have been even stronger, as decreased light penetration and soil temperatures below the ungrazed canopy (Semmartin and Oesterheld 2001) would have further reduced decomposer activity inside the exclosure. Alternatively, it is plausible that long-term cattle grazing had modified the soil environment for decomposition. Indeed, faster litter breakdown in the grazed site corresponded with higher standing levels of soil available N, which may reflect greater nutrient returns in animal faeces, deposition of readily decomposable plant litter, and higher net mineralisation rates (Seagle and McNaughton 1992; Chaneton et al. 1996; McNaughton et al. 1997; Tracy and Frank 1998). Nitrogen availability has been shown to enhance decomposer activity in fertilization experiments (Kemp et al. 1994; Knorr et al. 2005), especially where productivity is co-limited by N and P as in the study grassland (Semmartin et al. 2007). While the precise mechanisms are beyond the scope of this study, based on evidence from other systems, we hypothesise that changes in the soil microbial community might be involved in the observed differences in shoot litter turnover between grazed and ungrazed sites (Bardgett et al. 1998, 2001).

In conclusion, we have shown that the influence of large herbivores on decomposition processes induced through site conditions was more consistent than that mediated by the quality of litter shed by two grazing-tolerant grasses. Aboveground litter release of N and P was stimulated in grazed grassland irrespective of litter species and origin, suggesting that the soil environment outweighed litter chemical attributes as a control of decomposition in this system. As predicted by current models (e.g. Bardgett and Wardle 2003), grazing effects on nutrient cycling mediated by litter quality changes did occur but were idiosyncratic for two co-occurring grasses. We showed that, at the intraspecific level, prior grazing can either enhance or retard shoot litter decomposition and nutrient mineralisation. Such species-specific effects of grazing on litter functional attributes might relate to the photosynthetic metabolism (C_3 vs C_4, see Kemp et al. 1994) and N economy of the plants involved, a proposal that needs further investigation. In contrast, we provided strong evidence that grazing history exerted no apparent effect on nutrient cycling through root litter pools. This finding (see also Biondini and Manske 1996; Moretto et al. 2001) makes it clear that care must be taken when modeling belowground litter compartments to explore grazing impacts on carbon and nutrient cycling at the whole ecosystem level.

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