Austral ECOLOGY A Journal of ecology in the Southern Hemisphere
Ecological Society of Australia

Austral Ecology (2010) ••, ••–••

Does decomposition of standard materials differ among grassland patches maintained by livestock?

MARÍA VICTORIA VAIERETTI,[1]* ANA M. CINGOLANI,[1,2] NATALIA PÉREZ HARGUINDEGUY,[1,2] DIEGO E. GURVICH[1,2] AND MARCELO CABIDO[1,2]

[1]*Instituto Multidisciplinario de Biología Vegetal (CONICET-Universidad Nacional de Córdoba). CC 495, 5000 Córdoba (Email: vvaieretti@imbiv.unc.edu.ar), and* [2]*Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Córdoba, Argentina*

Abstract Grazing can modify vegetation structure and species composition through selective consumption, modifying plant litter quality and hence decomposability. In most grasslands, moderate stocking rates maintain a mosaic of high-quality patches, preferentially used by herbivores ('grazing lawns'), and low-quality tall patches, which are avoided. In grazing lawns decomposition rates can be accelerated because of the higher litter quality of its component species and, besides, through the indirect effect of increased nutrient availability in soil. We aimed at testing this indirect effect using standard materials, comparing their decomposition in grazing lawns, open and closed tall tussock grasslands. We selected 10 patches of each type and sampled floristic composition, soil variables and cattle dung deposition. Standard materials were filter paper and *Poa stuckertii* litter. We prepared litterbags of 0.3 mm (thin mesh) and 1 mm mesh size (coarse mesh). Samples were incubated for 65 days in two ways: above-ground (thin and coarse mesh) and below-ground (only thin mesh), aiming at analysing the conditions for decomposition for surface litter and buried litter or dead roots, respectively. Physical and chemical soil variables did not differ among patch types, despite the differences in species composition. Closed tussock grasslands showed the lowest dung deposition, confirming the less intense use of these patches. Soil nitrogen availability ($N\text{-}NO_3^-$ and $N\text{-}NH_4^+$) was not significantly different among patch types. Each standard material followed a different decomposition pattern across patch types. For above-ground incubated samples, *Poa* litter decomposed significantly faster in lawns, and slower in open tussock grasslands. Filter paper decomposed significantly faster in closed tussock grasslands than in the other two patch types. Decomposition of below-ground incubated samples did not significantly differ among patch types, in line with results for soil variables. Above-ground differences in decomposition may be associated with differences in microclimatic conditions resulting from differences in vegetation structure.

Key words: above-ground, below-ground, decomposition, grazing, nutrient cycling, vegetation patch.

INTRODUCTION

Grazing can modify vegetation structure and species composition through selective consumption and altered competitive interactions (Milchunas & Lauenroth 1993). The change in vegetation structure and composition produced by grazing is, generally, not homogeneous in space. In ecosystems, not strongly limited by soil nutrients and water, grazing at moderate stocking rates maintains a mosaic of short and tall vegetation patches (McNaughton 1984; Jaramillo & Detling 1988; Coughenour 1991). Short vegetation patches ('grazing lawns') are dominated by hervibory-tolerant plants with high tissue quality, and are preferentially used by herbivores, while tall grasslands have plants with lower tissue quality and are avoided by herbivores (Adler *et al.* 2001; Cingolani *et al.* 2005; McIntyre & Tongway 2005; Mcivor *et al.* 2005). These modifications in vegetation structure and the associated animal distribution patterns can be linked to changes in ecosystem processes (Bardgett & Wardle 2003).

Several studies have demonstrated that litter decomposition rates in moderately or heavily grazed sites can be accelerated, in relation to less grazed or ungrazed sites, through different mechanisms (Mcnaughton *et al.* 1997; Bardgett *et al.* 1998; Hamilton & Frank 2001; Bardgett & Wardle 2003). Decomposition rate can be favoured because grazing promotes the input of high-quality materials to soil, such as dung and urine, root exudates (which increase in response to herbivory) and more decomposable litter as a result of the livestock-induced changes in plant composition. These mechanisms may enhance soil nutrient availability, creating a highly favourable soil environment for decomposers. In this way, microbial activity and decomposition rates can be further stimulated (Bardgett *et al.* 1998; Hamilton & Frank 2001; Wardle *et al.* 2004).

---

*Corresponding author.

Accepted for publication November 2009.

doi:10.1111/j.1442-9993.2009.02105.x

The direct effect of herbivory on decomposition, produced by the input of high litter quality in heavily grazed sites compared with less grazed (or ungrazed) sites, has been repeatedly demonstrated (e.g. Holland & Detling 1990; Pastor *et al.* 1993; Bardgett *et al.* 1998; Olofsson & Oksanen 2002; Wardle *et al.* 2002). However, the indirect effect of herbivory, through an improved soil environment for decomposers, has been far less demonstrated. In this paper, we aimed at testing this indirect effect of herbivory on decomposition in grasslands of Pampa de Achala (central Argentina). In these grasslands livestock maintain vegetation patches with different physiognomies (grazing lawns, open and closed tall tussock grasslands) and different grazing pressure (Pucheta *et al.* 1998a; Cingolani *et al.* 2003, 2004). Previous studies in this system suggest that in grazing lawns nutrient cycling may be accelerated in relation to tussock grasslands. For example, Pucheta *et al.* (1998a) reported high N contents and low C : N ratios in aerial biomass of lawns compared with ungrazed tussock grasslands. Vendramini *et al.* (2000) reported similar results for the dominant species in both situations. Additionally, Pucheta *et al.* (2004) found that 95% of the root biomass was renewed per year in a grazing lawn, compared with 56% renewed in ungrazed tussock grasslands. Based on these and other studies (Bardgett *et al.* 1998; Hamilton & Frank 2001; Bardgett & Wardle 2003), we hypothesize that: (i) heavy use by livestock improves the environment for decomposers (as a result of increased soil nutrient availability) in lawns, compared with adjacent lightly grazed closed tussock grasslands; and (ii) open tussock grasslands may represent an intermediate situation. Accordingly, we expect to find the highest soil N availability, and the highest decomposition rates of standard materials, in grazing lawns, while the lowest values of these parameters should be recorded in adjacent closed tussock grassland. We expect to find the same decomposition patterns for samples incubated above- and belowground.

METHODS

Study area

The study was conducted in the upper grasslands belt of the Córdoba Mountains, in central Argentina (31°37′S, 64°48′W). The area comprises different landscape units, including valley bottoms and ravines, and plateaus with different degree of dissection. Soils are mollisols derived from the weathering of the granitic substrate and fine-textured eolian deposits (Cabido *et al.* 1987). At 2200 m a.s.l., mean annual temperature is 8°C with a winter absolute minima of −15°C, and no frost-free period. Mean annual precipitation is 924 mm, with most rainfall concentrated in the warmer months, between October and April (Cabido 1985; Colladon 2008). The main economic activity in the region is livestock raising, which started at the beginning of the 17th century. Livestock, mainly cattle and sheep, completely replaced large native herbivores by the beginning of the 20th century (Díaz *et al.* 1994). The large size of the paddocks allows animals to select between different landforms and plant communities (Cingolani *et al.* 2003).

Landscape in the region is a mosaic of *Polylepis australis* BITT woodlands, tussock grasslands, grazing lawns, erosion pavements and granite outcrops (Cingolani *et al.* 2004). Grasslands and lawns patches comprise three distinct physiognomies, lawns, open tussock grasslands and closed tussock grasslands (Pucheta *et al.* 1997; Cingolani *et al.* 2005). The lawn patches are dominated by short palatable plants with high foliar nutrient content, and traits that suggest high relative growth rates. Open tussock grasslands comprise a mixture of short vegetation and tussock species, while closed tussock grassland patches are strongly dominated by tall tussock species (Pucheta *et al.* 1998a; Cingolani *et al.* 2003, 2007). Livestock pressure is increasingly higher as the proportion of short vegetation in the patch increases, from closed tussock grasslands to grazing lawns (A. von Müller 2009, unpubl. data).

While the mechanism of formation of lawn patches is still debated, they are in fact maintained by herbivory, as indicated by their conversion to tall grasslands when herbivory is excluded (Pucheta *et al.* 1998a, b; Cingolani *et al.* 2003; M. V. Vaieretti 2009, unpubl. data).

The study was performed in the Quebrada del Condorito National Park, where domestic livestock was maintained in some areas to preserve local biodiversity (Teich *et al.* 2005). Sampling was performed on a gently dissected plateau, in a large paddock (1514 ha) under moderate cattle grazing (0.20–0.25 Cattle Equivalents per ha of vegetated land, i.e. discounting rock surface). We selected a representative area of about 225 ha within the paddock. In this area we chose 10 different sites (about 15 × 15 m) for each of the three vegetation patch types (lawn, open tussock grassland and closed tussock grassland). All sites were located at similar altitudes a.s.l. (2150–2200) and on gentle slopes (1–5%). Sites were distributed across the dominant topographic positions present in the area, from lower to upper slopes.

Characterization of sampling sites

In order to describe vegetation, in February 2006 we performed a floristic survey (4 m × 4 m plots) in each

doi:10.1111/j.1442-9993.2009.02105.x

of the 30 selected sites. All vascular plants were recorded and their percent cover visually estimated. At each site we measured maximum vegetation height in 20 randomly placed 625 cm^2 quadrates. Soil depth was recorded at four random locations per site, and then averaged. Additionally, for each site a soil compound sample of the upper horizon (0–15 cm) was collected. We measured soil texture (Day 1986), pH (Thomas 1996), organic C (%) by Walkley–Black technique (Nelson & Sommers 1996), total N (%) by Kjeldahl technique (Bremner 1996), extractable P (ppm) by Bray & Kurtz N°1 technique (Kuo 1996), cationic exchange capacity (Cationic Exchange Capacity (CEC) meq/100 g) and cations (Ca^{++}, Na^+, Mg^{++} and K^+ meq/100 g) (Sumner & Miller 1996). We also measured soil nitrogen availability: $N\text{-}NO_3^-$ (ppm) and $N\text{-}NH_4^+$ (ppm) by *Direct Potentiometer* (Mulvaney 1996).

Additionally, and in order to corroborate that patch types indeed differ in animal utilization, we measured cattle dung deposition at each site by counting the presence of dung in 50 randomly placed 30 cm × 30 cm quadrats, expressing dung frequency as a percentage. This measure is an indirect way to estimate both the grazing pressure (Cingolani *et al.* 2002; Teich *et al.* 2005) and the inputs through faeces to soil.

Decomposition experiments

To determine the environmental quality for potential decomposers, at each site we incubated standard substrates. Standard substrates are widely used (Binkley 1984; O'lear *et al.* 1996) because they provide important insights about the effect of the environment on decomposition, independent of the substrate quality (Jenny *et al.* 1949; Tsarik 1975; Piene & Van Cleve 1978; Orwin *et al.* 2006). The standard substrates selected were filter paper (Berg & Lawskoski 2006) and *Poa stuckertii* (Hack.) Parodi litter ('*Poa* litter'), an abundant species in the study area. To account for possible variability in *Poa* litter quality across sites, this material was randomly collected across all the sites within the study area and then pooled.

Samples were prepared following the widely used litterbag technique. Litterbags were made of 0.3 mm mesh nylon ('thin mesh') and were filled with 3 g of air-dried standard materials. Although it is possible that the small mesh size could reduce access to soil fauna (Seastedt 1984; Bradford *et al.* 2002), it helped to prevent excessive loss of material, particularly *Poa* litter, during bag manipulation. To control if mesh size (and thus the differential access to soil mesofauna) could substantially influence our results, we also prepared 1 mm mesh size litterbags ('coarse mesh').

To compare the above-ground and below-ground decomposition conditions among different patch types, samples were incubated in two ways: buried (only samples of thin mesh, five per site for each material) and not-buried (five samples of thin mesh and five samples of coarse mesh for each site and material) for 65 days, from December 2005 to March 2006. The incubation period was established based on previous studies in the region, aiming at covering both the first and the intermediate stages of decomposition (Pérez harguindeguy *et al.* 2000; Vaieretti *et al.* 2005; Pérez harguindeguy *et al.* 2007). Buried samples were located at 5 cm below-ground, and covered with litter and soil mixture. Unburied samples were fixed to the soil with stakes and protected with barbed wire to avoid damage by cattle and small animals. After incubation, samples were stored at −14°C until processing. Once defrosted, adhering soil, soil fauna and other extraneous materials were removed by brushing or swiftly rinsing with water. Samples were oven-dried for at least 48 h at 60°C, and then weighed. Decomposition of each sample was estimated as the percentage of dry weight loss at the end of the incubation period (Cornelissen 1996; Cornelissen *et al.* 1999). Samples were averaged to obtain one value per site (replicate). For both materials, initial dry weight was calculated from the water content of a subsample that was weighed at the same time as the samples, oven-dried until constant weight at 60°C and then reweighed.

Data analyses

To corroborate that the visual differences in physiognomies between the three patch types were consistent with species composition variation as indicated by the literature (Pucheta *et al.* 1997; Cingolani *et al.* 2003), we performed a Detrended Correspondence Analysis using the 'site × species' abundance matrix. To analyse differences in vegetation height across physiognomies, we used one-way ANOVA and *post hoc* comparison performed with a Tukey test ($P < 0.05$).

We described the variation in soil properties across sites through Principal Component Analysis (PCA). We used the following variables: texture (sand, clay and silt %), pH, organic C (%), total N (%), C : N ratio, extractable P (ppm), CEC (meq/100 g), cations (Ca^{++}, Na^+, Mg^{++} y K^+ meq/100 g) and soil depth (cm). Through this analysis we obtained two main axes that summarized soil properties variation. To analyse if the three patch types differed in soil characteristics, besides the visual examination of the PCA plot, we compared the scores in each main axis (PCA axis 1 and PCA axis 2) and each soil variable independently, between the three patch types, using one-way ANOVAs. The same analysis was used to compare dung deposition among patch types.

doi:10.1111/j.1442-9993.2009.02105.x

To analyse differences in soil nitrogen availability, we compared the N-NO_3^- (ppm) and N-NH_4^+ (ppm) soil content between patch types with one-way ANOVAs. To compare the decomposition rate of the different standard materials (filter paper and *Poa* litter) between mesh sizes (thin and coarse) and patch types for samples incubated above-ground, we used repeated measures ANCOVAs, with the plot as the subject variable, the mesh size as a within-factor, and patch type as a between-factor. We included both PCA axes as co-variables (to control for soil properties independently of patch types). To compare the decomposition rate of each material incubated below-ground, we used ANCOVAs, with patch type as the main factor and both PCA axes as co-variables. In all cases, when a co-variable or factor was not significant, it was discarded from the model.

Finally, we used Pearson correlations to test pairwise relationships between decomposition of different materials (filter paper, *Poa* litter), incubation conditions (above-ground, below-ground) and nitrogen availability (N-NO_3^-, N-NH_4^+).

RESULTS

Patch types characterization

As expected, the three patch types were clearly segregated in the space defined by axes 1 (eigenvalue 0.76) and 2 (eigenvalue 0.28) of the Detrended Correspondence Analysis (plot not shown), indicating that floristic composition differed among physiognomies. Lawns were dominated by forbs and graminoids (short grasses, rushes and sedges), while open tussock grasslands were dominated by tussock grasses, forbs and short graminoids. Closed tussock grasslands were strongly dominated by *Deyeuxia hieronymi* (Hack.) Türpe and *Poa stuckertii* (Hack.) Parodi tussocks (Table 1). Vegetation height was significantly different among the three patch types ($F_{2,\,27} = 343.6$; $P < 0.001$). Mean values were 6 cm in the lawns, 36 cm in the open tussock grasslands and 73 cm in the closed tussock grasslands, in line with the differences in plant composition.

Soil characteristics were not associated with vegetation structure, but presented high variability within patch types, in line with previous studies (Cingolani *et al.* 2003). The results obtained through the PCA analysis were confirmed through ANOVAs, which showed that neither the position along both axes nor any individual soil variables were significantly different among patch types ($P > 0.05$, Table 2). Axes 1 and 2 of the PCA analysis explained 27% and 22% of the variance, respectively. The sites with highest sand soil content were located in the negative side of axis 1, and the sites with highest soil clay and Ca^{++} content, and the highest CEC were in the positive side. Axis 2 separated the sites with highest pH and K^+ content to the positive side from those with highest silt, organic C and total N to the negative side (Fig. 1a). All patch types were intermingled along the axes (Fig. 1b).

Dung frequency was higher in lawns and open tussock grasslands (29 and 30 %, respectively), than in closed tussock grasslands where dung frequency was less than half of that recorded in the other patches (13 %, $F_{2,\,27} = 4.65$; $P < 0.05$).

Table 1. Mean cover (%) for each patch type of the most abundant species

Vegetation characteristics	Patch type Lawns	 Open tussock grasslands	 Closed tussock grasslands
Annual graminoids			
Muhlenbergia peruviana (P Beauv.) Steud.	6.4	0.2	0.02
Perennial graminoids			
Carex fuscula d' Urv.	14.1	5	0.04
Eleocharis albibracteata Nees & Meyen ex Kunth	14.3	0	0
Juncus uruguensis Griseb.	7.9	0.6	0
Forbs			
Adesmia bicolor *(Poir.) DC.*	1.5	2	0
Alchemilla pinnata *Ruiz & Pav.*	37.7	9	1.6
Briza subaristata Lam.	0.1	2	0.04
Eringyum agavifolium Griseb.	6.4	10	3.8
Eringyum nudicaule Lam.	2	4	0
Tussock grasses			
Deyeuxia hieronymi (Hack.) Türpe	2.4	50	21.3
Festuca circinata Griseb.	5.8	0.01	0
Poa stuckertii (Hack.) Parodi	0.3	8	71

Table 2. Soil variables (mean ± SE) in the three patch types

Soil variables	Lawns	Open tussock grasslands	Closed tussock grasslands
	Patch type[†]		
Organic C (%)	6.1 (0.52)	5.9 (0.47)	5.8 (0.42)
Total N (%)	0.5 (0.05)	0.5 (0.04)	0.5 (0.04)
C : N	13.2 (0.97)	12.3 (0.32)	12.2 (0.41)
P (ppm)	1.8 (0.65)	2.1 (0.16)	2 (0.25)
pH	4.9 (0.10)	4.9 (0.09)	5 (0.07)
Ca (meq/100 g)	10.2 (1.71)	11.2 (1.08)	14.3 (1.75)
Mg (meq/100 g)	1.9 (0.28)	1.5 (0.17)	1.3 (0.17)
Na (meq/100 g)	0.3 (0.05)	0.2 (0.03)	0.2 (0.03)
K (meq/100 g)	0.3 (0.02)	0.4 (0.04)	0.4 (0.03)
CEC (meq/100 g)	17.9 (2.41)	18.5 (1.27)	23 (2.12)
Clay (%)	13.9 (1.39)	14.6 (0.66)	16.4 (1.26)
Silt (%)	32.2 (1.45)	32.9 (1.10)	33.3 (1.50)
Sand (%)	53.9 (2.11)	52.5 (1.47)	50.3 (0.82)
Soil depth (cm)	54.6 (7.47)	60.1 (6.74)	74.7 (7.43)

[†]None of the soil variables differed significantly among patch types (ANOVA, $P > 0.05$). CEC, Cationic Exchange Capacity.

Soil nitrogen availability and decomposition patterns

Soil available nitrogen measured as N-NO_3^- content tended to be lower in the lawns than in the open and closed tussock grasslands, but differences were not significant (Fig. 2). Soil N-NH_4^+ content was also lowest in the lawns, but again differences were not significant ($P > 0.05$; Fig. 2).

Mean decomposition (dry weight loss) of both materials (*Poa* litter and filter paper) incubated above-ground differed among patch types, but did not differ between mesh sizes, nor was the interaction between mesh size and patch type significant ($P > 0.05$). Consequently, we discarded the within-factor mesh size and repeated the analysis using standard ANCOVAs with the average decomposition between both mesh sizes as the dependent variable, patch type as the main factor and both PCA axes as co-variables. Both materials followed a different pattern of decomposition across patch types (Fig. 3a). The highest decomposition of *Poa* litter was found in lawns and the lowest in open tussock grasslands ($F_{2,\,26} = 20.17$; $P < 0.001$). In turn, filter paper decomposed significantly faster in closed tussock grasslands than in the other two patch types ($F_{2,\,27} = 6.45$; $P = 0.005$). For *Poa* litter, PCA axis 1 was significant ($P < 0.05$) indicating that within each patch type, decomposition was faster in more fine-textured soils. For filter paper neither co-variable was significant. In accordance with these results, decomposition patterns of *Poa* litter and filter paper incubated above-ground were not correlated (Table 3).

In contrast to the results for above-ground incubated samples, decomposition of below-ground incubated samples (only thin mesh) did not differ among patch types (Fig. 3b). The co-variables (PCA axis 1 and 2) were not significant in any case. Once more, decomposition patterns of *Poa* litter and filter paper incubated below-ground were not correlated (Table 3). Although we did not find significant differences between patch types in *Poa* litter samples incubated below-ground, their pattern of decomposition was positively correlated ($P < 0.05$) with decomposition of *Poa* litter samples incubated above-ground (Table 3).

To be sure that the differences between the results obtained for above-ground and below-ground samples were not caused by the higher power of our above-ground tests (because each above-ground sample was obtained from 10 instead of 5 subsamples), we repeated the analyses using thin and coarse mesh sizes separately, and the above-ground differences among patch types remained significant in all cases.

Dry weight loss of *Poa* litter and filter paper, incubated both above-ground and below-ground, was not significantly correlated with soil N-NO_3^- or N-NH_4^+ content (Table 3).

DISCUSSION

Contrary to our predictions based on literature (Bardgett *et al.* 1998; Hamilton & Frank 2001; Bardgett & Wardle 2003), we did not find that heavy livestock pressure increased soil nutrient availability in lawns compared with adjacent less grazed tall tussock grasslands. Additionally, we did not find that patterns of decomposition in the different patch types were related to nutrient availability. According to the literature, the acceleration of decomposition in grazing lawns compared with tall grasslands (as a consequence of increased dung and urine, root exudates and a

doi:10.1111/j.1442-9993.2009.02105.x

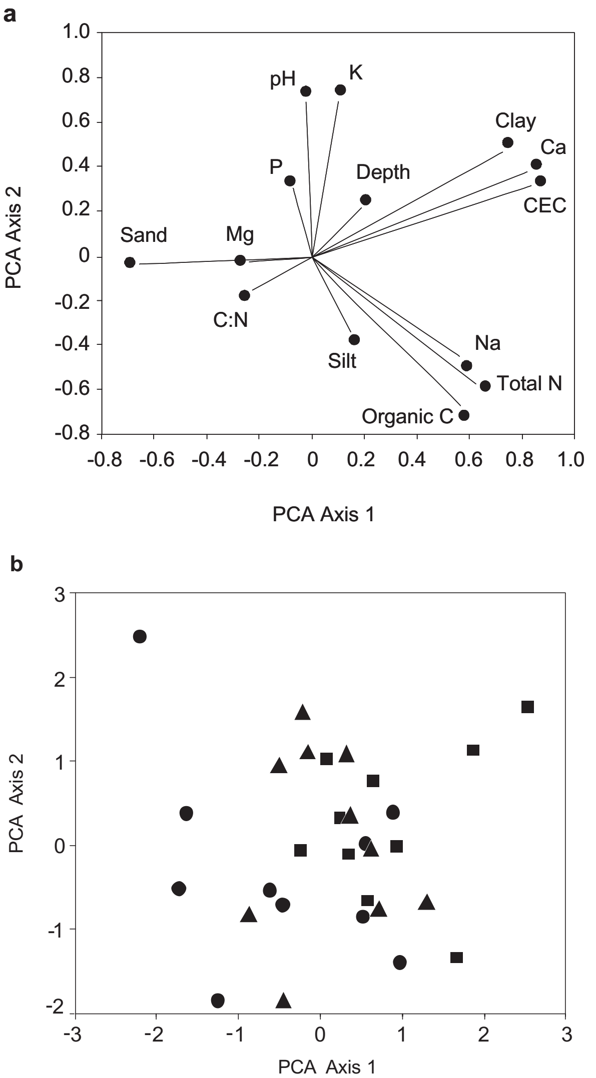

Fig. 1. Diagrams of Principal Component Analysis (PCA) ordination of the 30 selected sites as a function of soil variables. (a) Contribution of soil variables. (b) Ordination of sites. Different symbols represent different patch types, ●: Lawns, ▲: Open Tussock Grasslands and ■: Closed Tussock Grasslands.

higher litter quality in these patch types), should increase nutrient availability in soil, thus stimulating decomposition even more. We found an increase in dung deposition in lawns (but also in open tussock grasslands), while previous studies have also found an increase in their leaf quality (Pucheta *et al.* 1998a; Cingolani *et al.* 2003, 2007). However, this was not translated to an increase in soil nutrient availability, nor was it correlated with the observed pattern of decomposition. Although decomposition of *Poa* litter incubated above-ground was highest in lawns as expected, it was also high in closed tussock grasslands, and lowest in open tussock grasslands. In the case of filter paper incubated above-ground, and for both materials incubated below-ground, the patterns were even more different than expected. In the below-ground case, results were completely unexpected because decomposition rates between patches showed no differences at all. As mentioned above, although lawns and open grasslands were effectively more used by grazers than closed grasslands (dung deposition was twice higher in lawns and open tussock grasslands than in closed tussock grasslands), this did not show a correlation with the pattern of soil nutrient availability. In other words, although the patterns of decomposition partially agreed with our predictions, the mechanisms proposed in the literature as determinants of faster decomposition in lawns compared with tall grasslands, seem not to be the main determinants of decomposition in Pampa de Achala grasslands.

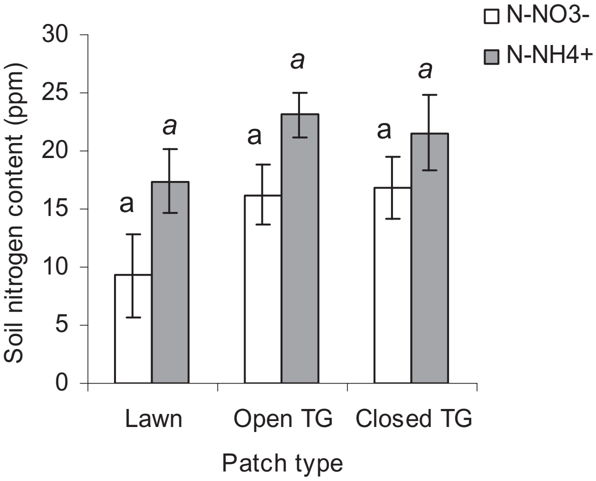

Fig. 2. Soil nitrate and ammonium content in three selected patch types. Bars represent mean values ± 1 SE ($n = 10$). Similar letters indicate no significant difference among patch types within each ion (designated by different font types) at $P < 0.05$. TG, tussock grasslands.

In view of the lack of association between soil nutrient availability and decomposition patterns, and the lack of differences in below-ground decomposition across patch types, we propose alternative mechanisms. For above-ground decomposition, we propose that microclimate may be the main determinant of decomposition. In lawns, which have significantly less standing plant biomass, soil temperature and moisture can be different from those in closed tussock grasslands (LeCain *et al.* 2000). This difference may not only be restricted to mean temperatures and soil moisture, but also to diurnal and seasonal variations, as lawns have lower temperature inertia (McNaughton 1984, 1985; Seastedt *et al.* 1988; Posse *et al.* 2000; Yates *et al.* 2000), and probably lower soil moisture inertia as well. As a result, lawns can be warmer in summer (and in daytime), and colder in winter (and at night) than

doi:10.1111/j.1442-9993.2009.02105.x

closed tussock grasslands, perhaps more stable habitats (Posse *et al.* 2000; Yates *et al.* 2000). Additionally, the higher soil trampling in lawn patches (Cingolani *et al.* 2003), combined with higher temperatures, could reduce infiltration and enhance evaporation. Consequently, water availability can be reduced, limiting microbial activity (Naeth *et al.* 1991). The net balance between all these micro-environmental changes, involving plant structure, herbivore use and its consequences to microbial activity, is difficult to predict and can be responsible for the surprising decomposition patterns obtained.

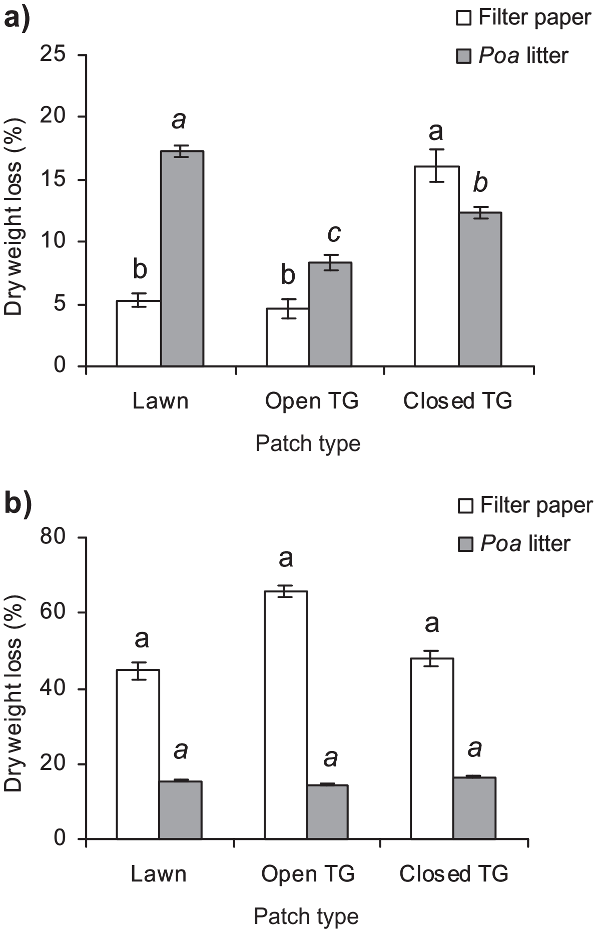

Fig. 3. Filter paper and *Poa* litter dry weight loss (%) for, (a) above-ground incubated samples and, (b) below-ground incubated samples in the three selected patch types. Bars represent mean values ± 1 SE ($n = 10$). Different letters indicate significant differences among patch types within each standard material (designated by different font types) at $P < 0.05$. TG, tussock grasslands.

The mechanisms proposed as regulators of above-ground decomposition would not be operating a few centimetres below the soil surface (Bardgett & Wardle 2003; Wardle *et al.* 2004). While surface temperature and moisture are highly variable, below-ground soil temperature and moisture are probably more similar among patch types (Yates *et al.* 2000; Voroney 2007).

It should be noted that the two standard materials used in the experiments did not follow the same decomposition patterns, in particular for samples incubated above-ground. Clearly, the quality of each material influenced their decomposition but also interacted with the micro-environmental conditions of the different patches. As mentioned above, grazing prevents the colonization of the lawns by tussocks, and maintained vegetation short enough through plant biomass removal and trampling. Because of this, the soil surface of grazing lawns is more exposed to ultraviolet-B radiation, which can affect litter decomposition by stimulating lignin degradation (Austin & Vivanco 2006). This would differentially affect *Poa* litter (accelerating its decomposition), because filter paper lacks this component. In closed tussock grasslands the effect of the large amounts of aerial biomass and accumulated litter (Pucheta *et al.* 1997; Vaieretti *et al.* 2010, unpubl. data) would prevent photodegradation of *Poa* litter, but at the same time, it could significantly increase moisture content (LeCain *et al.* 2000) compared with lawns. This could enhance filter paper decomposition, and may also accelerate *Poa* litter decomposition in these patch types compared with open tussock grasslands. Considering the chemical composition of both standard materials (only cellulose in filter paper, and 'average leaf' composition in *Poa* litter), it is probable that *Poa* litter decomposition

Table 3. Pearson Correlation Coefficients (r) between % dry weight loss of filter paper and *Poa* litter above-ground and below-ground incubated; and N-NO_3^- and N-NH_4^+ soil content

	N-NH_4^+ (ppm)	N-NO_3^- (ppm)	*Poa* litter below-ground	filter paper below-ground	*Poa* litter above-ground†
filter paper above-ground†	0.14	0.09	0.25	–0.15	0.13
Poa *litter* above-ground†	0.07	–0.19	0.42*	–0.36*	–
Filter paper below-ground	0.31	–0.24	–0.21	–	
Poa litter below-ground	0.02	0.09	–		
N-NO_3^- (ppm)	0.19	–			

*$P < 0.05$; **$P < 0.01$ and ***$P < 0.001$. †Dry weight loss (%) of above-ground incubated samples with both mesh sizes were averaged per site for each material before performing the correlations.

doi:10.1111/j.1442-9993.2009.02105.x

would better represent the patterns for most species present in the area. This result makes the selection of the standard material more difficult than expected, and also implies that standard materials types should be taken into account when comparing studies.

We are aware that the effect of microclimatic conditions as interpreted in the paragraphs above may be highly speculative because other factors could also be influencing micro-environmental conditions. We are also aware that the patterns found are restricted to the summer season, when most decomposition occurs in this system, but not all. However, and in spite of the obvious value of general models predictions about grazing effect on decomposition rates, our results suggest that at local or reduced spatial scales, microclimatic control of decomposition (via vegetation structure), could be stronger than previously thought. As such, these factors could even mask the grazing control on decomposition through changes in soil nutrient availability, generally considered as the principal factor.

In summary, our results showed that in Pampa de Achala grasslands, where herbivory maintains vegetation patches with different structure, species composition and livestock pressure, these differences are not translated to better soil micro-environmental conditions for decomposition in the heavily grazed patches. The mechanisms proposed in the literature (Bardgett & Wardle 2003), which do not consider the interaction between vegetation quality and nutrient availability with microclimatic conditions, may not be applicable at the patch scale. At this scale, in Pampa de Achala grasslands, grazing effects through the return of feces and urine to soil and by maintaining higher litter quality species in lawns, may not result in higher soil nutrient availability and higher decomposition rates of the same material, compared with tussock grasslands. Future studies focused on a more detailed exploration of complex interactions involving climate and microclimate, litter quality, herbivory pressure, nutrient availability and resulting soil processes (for example, temperature and moisture measurements, decomposition *in situ* of litter mixtures from each patch and N mineralization measures), will allow the development of alternative models to explain the effects of herbivory on nutrient cycling at this scale.

ACKNOWLEDGEMENTS

Financial support for this work was provided by CONICET (6196/05), Ministerio de Ciencia y Técnica de la Provincia de Córdoba, Argentina, FONCYT – PICT 25712 and IAI CRN II 2005. We thank our working team for their assistance in the field and laboratory work, and to Daniel Renison for helping with the English version. We are grateful to the associate editor and three anonymous referees for critical comments and helpful suggestions which significantly improved this paper.

REFERENCES

Adler P. B., Raff D. A. & Lauenroth W. K. (2001) The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia* **128,** 465–79.

Austin A. T. & Vivanco L. (2006) Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation. *Nature* **442,** 555–8.

Bardgett R. D. & Wardle D. A. (2003) Herbivore-mediated linkages between aboground and belowground communities. *Ecology* **84,** 2258–68.

Bardgett R. D., Wardle D. A. & Yeates G. W. (1998) Linking above-ground and below-ground food webs: how plant responses to foliar hervibory influence soil organisms. *Soil Biol. Biochem.* **30,** 1867–78.

Berg B. & Lawskoski R. (2006) Methods in studies of organic matter decay. In: *Litter Decomposition: A Guide to Carbon and Nutrient Turnover* (ed. H. Caswell) pp. 291–300. Academic Press, Elsevier.

Binkley D. (1984) Does forest removal increase rates of decomposition and nutrient release? *For. Ecol. Manage.* **8,** 229–33.

Bradford M. A., Tordoff G. M., Eggers T., Jones T. H. & Newington J. E. (2002) Microbiota, fauna and mesh size interactions in litter decomposition. *Oikos* **99,** 317–23.

Bremner J. M. (1996) Nitrogen – total. In: *Methods of Soil Analysis. Part 3 – Chemical Methods* (ed. D. L. Sparks) pp. 1085–122. Chapter 37. ASA, SSSA, CSSA, Madison.

Cabido M. (1985) Las comunidades vegetales de la pampa de Achala, Sierras de Córdoba, Argentina. *Doc. Phytosociol.* **9,** 431–43.

Cabido M., Breimer R. & Vega G. (1987) Plant communities and associated soil types in a high plateau of the Córdoba mountains, Central Argentina. *Mt. Res. Dev.* **7,** 25–42.

Cingolani A. M., Anchorena J., Stoffella S. & Collantes M. B. (2002) A landscape – scale model for optimal management of sheep grazing in the Magellanic steppe. *Appl. Veg. Sci.* **5,** 159–66.

Cingolani A. M., Cabido M., Renison D. & Solís Neffa V. (2003) Combined effects of environment and grazing on vegetation structure in Argentine granite grasslands. *J. Veg. Sci.* **14,** 223–32.

Cingolani A. M., Renison D., Zak M. R. & Cabido M. (2004) Mapping vegetation in a heterogeneous mountain rangeland using Landsat data: an alternative method to define and classify land-cover units. *Remote Sens. Environ.* **92,** 84–97.

Cingolani A. M., Noy-Meir I. & Díaz S. (2005) Grazing effects on rangeland diversity: a synthesis of contemporary models. *Ecol. Applic.* **15,** 757–73.

Cingolani A. M., Cabido M., Gurvich D. E., Renison D. & Díaz S. (2007) Filtering processes in the assembly of plant communities: are species presence and abundance driven by the same traits? *J. Veg. Sci.* **18,** 911–20.

Colladon L. (2008) Anuario pluviométrico 1992–2005. In: *Cuenca del Río San Antonio. Sistema del río Suquía – Provincia de Córdoba*. Instituto Nacional del Agua y del Ambienten (INA) y Centro de Investigaciones de la Región Semiárida (CIRSA), Carlos Paz, Argentina.

Cornelissen J. H. C. (1996) An experimental comparison of leaf decomposition rates in a wide range of temperature plant species and types. *J. Ecol.* **84,** 573–82.

doi:10.1111/j.1442-9993.2009.02105.x

Cornelissen J. H. C., Pérez-Harguindeguy N., Díaz S. *et al.* (1999) Leaf structure and defense control litter decomposition rate across species and life forms in regional floras of two continents. *New Phytol.* **143,** 191–200.

Coughenour M. B. (1991) Spatial components of plant-herbivore interactions in pastoral, ranching and native ungulate ecosystems. *J. Range Manage.* **44,** 530–42.

Day P. R. (1986) Particle fractionation and particle-size analysis. In: *Methods of Soil Analysis, (Part I)* (ed. C. A. Black) pp. 545–67. American Society of Agronomy, Soil Science Society of America, Madison.

Díaz S., Acosta A. & Cabido M. (1994) Community structure in montane grasslands of central Argentina in relation to land use. *J. Veg. Sci.* **5,** 483–8.

Hamilton E. W. & Frank D. A. (2001) Can plant stimulate soil microbes and their own nutrient supply? Evidence from a grazing tolerant grass. *Ecology* **82,** 2397–402.

Holland E. & Detling J. K. (1990) Plant response to herbivory and belowground nitrogen cycling. *Ecology* **71,** 1040–9.

Jaramillo V. J. & Detling J. K. (1988) Grazing history, defoliation and competition: effects on shortgrass production and nitrogen accumulation. *Ecology* **69,** 1599–608.

Jenny H., Gessel S. P. & Bingham F. T. (1949) Comparative study of decomposition of organic matter in temperate and tropical regions. *Soil Sci.* **68,** 419–32.

Kuo S. (1996) Phosphorus. In: *Methods of Soil Analysis. Part 3 – Chemical Methods* (ed. D. L. Sparks) pp. 869–920. Chapter 32. ASA, SSSA, CSSA, Madison.

LeCain D. R., Morgan J. A., Schuman G. E., Reefer J. D. & Hart R. H. (2000) Carbon exchange rates in grazed and ungrazed pastures of Wyoming. *J. Range Manage.* **53,** 199–206.

McIntyre S. & Tongway D. (2005) Grassland structure in native pastures: links to soil surface condition. *Ecol. Manage. Rest.* **6,** 43–50.

McIvor J. G., McIntyre S., Saeli I. & Hodgkinson J. J. (2005) Patch dynamics in grazed subtropical native pastures in south-east Queensland. *Austral Ecol.* **30,** 445–64.

McNaughton S. J. (1984) Grazing lawns: animals in herds, plant form and coevolution. *Am. Nat.* **124,** 863–86.

McNaughton S. J. (1985) Ecology of a grazing ecosystem: the Serengeti. *Ecol. Monogr.* **55,** 259–94.

McNaughton S. J., Banyikwa F. F. & McNaughton M. M. (1997) Promotion of the cycling of diet-enhancing nutrients by African grazers. *Science* **278,** 1798–800.

Milchunas D. G. & Lauenroth W. K. (1993) A quantitative assessment of the effects of grazing on vegetation and soils over a global range of environments. *Ecol. Monogr.* **63,** 327–66.

Mulvaney R. L. (1996) Nitrogen – inorganic forms. In: *Methods of Soil Analysis. Part 3 – Chemical Methods* (ed. D. L. Sparks) pp. 1123–84. Chapter 38. ASA, SSSA, CSSA, Madison.

Naeth M. A., Chanasyk D. S., Rothwell R. L. & Bailey A. W. (1991) Grazing impacts on soil water in mixed prairie and fescue grassland ecosystems of Alberta. *Can. J. Siol Sci.* **71,** 313–25.

Nelson D. W. & Sommers L. E. (1996) Total carbon, organic carbon, and organic matter. In: *Methods of Soil Analysis. Part 3 – Chemical Methods* (ed. D. L. Sparks) pp. 961–1010. Chapter 34. ASA, SSSA, CSSA, Madison WI.

O'Lear H. A., Seastedt T. R., Briggs J. M., Blair J. M. & Ramundo R. A. (1996) Fire and topographic effects on decomposition rates and nitrogen dynamics of buried wood in tallgrass prairie. *Soil Biol. Biochem.* **28,** 322–9.

Olofsson J. & Oksanen L. (2002) Role of litter decomposition for the increased primary production in areas heavily grazed by reindeer: a litterbag experiment. *Oikos* **96,** 507–15.

Orwin K. H., Wardle D. A. & Greenfield L. G. (2006) Ecological consequences of carbon substrate identity and diversity in a laboratory study. *Ecology* **87,** 580–93.

Pastor J., Dewey B., Naiman R., McInnes P. & Cohen Y. (1993) Moose browsing and soil fertility in the boreal forest of Isle Royale national park. *Ecology* **74,** 467–80.

Pérez Harguindeguy N., Díaz S., Cornelissen J. H. C., Vendramini F., Cabido M. & Castellanos A. (2000) Chemistry and toughness predict leaf litter decomposition rates over a wide spectrum of functional types and taxa in central Argentina. *Plant Soil* **218,** 21–30.

Pérez Harguindeguy N., Díaz S., Vendramini F. *et al.* (2007) Direct and indirect effects of climate on decomposition in native ecosystems from central Argentina. *Austral Ecol.* **32,** 749–57.

Piene H. & Van Cleve K. (1978) Weight loss of litter and cellulose bags in a thinned white spruce forest in interior Alaska. *Can. J. For. Res.* **8,** 42–6.

Posse G., Achorena J. & Collantes M. B. (2000) Spatial micropatterns in the steppe of Tierra del Fuego induced by sheep grazing. *J. Veg. Sci.* **11,** 43–50.

Pucheta E., Cabido M. & Díaz S. (1997) Modelos de estados y transiciones para los pastizales de altura de las sierras de Córdoba, Argentina. *Ecotrópicos* **10,** 151–60.

Pucheta E., Cabido M., Díaz S. & Funes G. (1998a) Floristic composition, biomass, and aboveground net plant production in grazed and protected sites in a mountain grassland of central Argentina. *Acta Oecol.* **19,** 97–105.

Pucheta E., Vendramini F., Cabido M. & Díaz S. (1998b) Estructura y funcionamiento de un paztizal de montaña bajo pastoreo y su respuesta luego de su exclusión. *Rev. Agron. La Plata* **103,** 77–92.

Pucheta E., Bonamici I., Cabido M. & Díaz S. (2004) Belowground biomass and productivity of grazed site and a neighbouring ungrazed exclosure in a grassland in central Argentina. *Austral Ecol.* **29,** 201–8.

Seastedt T. R. (1984) The role of microarthropods in decomposition and mineralization processes. *Annu. Rev. Entomol.* **29,** 25–46.

Seastedt T. R., Ramundo R. A. & Hayes D. C. (1988) Maximisation of densities of soil animals by foliage herbivory: empirical evidence, graphical and conceptual models. *Oikos* **51,** 243–8.

Sumner M. E. & Miller W. P. (1996) Cation exchange capacity and exchange coefficients. In: *Methods of Soil Analysis. Part 3 – Chemical Methods* (ed. D. L. Sparks) pp. 1201–30. Chapter 40. ASA, SSSA, CSSA, Madison.

Teich I., Cingolani A. M., Renison D., Hensen I. & Giorgis M. (2005) Do domestic herbivores retard *Polylepis australis* Bitt. woodland recovery in the mountains of Córdoba, Argentina? *For. Ecol. Manage.* **219,** 229–41.

Thomas G.W. (1996) Soil pH and soil acidity. In: *Methods of Soil Analysis. Part 3 – Chemical Methods* (ed. D. L. Sparks) pp. 475–90. Chapter 16. ASA, SSSA, CSSA, Madison.

Tsarik I. (1975) Decomposition of cellulose in the litter layer and soil of *Pinus mugo* elfin woodland in the Ukrainian Carpathians. *Lesvedenie* **1,** 88–90.

Vaieretti M. V., Pérez Harguindeguy N., Gurvich D. E., Cingolani A. M. & Cabido M. (2005) Decomposition dynamics and physico-chemical leaf quality of abundant species in a montane woodland in central Argentina. *Plant Soil* **278,** 223–34.

Vendramini F., Díaz S., Pérez Harguindeguy N., Cabido M., Llano-Sotelo J. M. & Castellanos A. (2000) Composición química y caracteres foliares en plantas de distintos tipos funcionales del centro-oeste de Argentina. *Kurtziana* **28,** 181–93.

Voroney R. P. (2007) The soil habitat. In: *Soil Microbiology, Ecology and Biochemistry* (ed. E. A. Paul) pp. 25–49. Chapter 2. Academis Press, Elsevier, UK.

Wardle D. A., Bonner K. I. & Barker G. M. (2002) Linkages between plant litter decomposition, litter quality, and vegetation responses to herbivores. *Funct. Ecol.* **16,** 585–95.

Wardle D. A., Bardgett R. D., Klironomos J. N., Setälä H., van der Putten W. H. & Wall D. H. (2004) Ecological linkages between aboveground and belowground biota. *Science* **304,** 1629–33.

Yates C. J., Norton D. A. & Hobbs R. J. (2000) Grazing effects on plant cover, soil and microclimate in fragmentes woodlands in south-western Australia: implications for restoration. *Aust. Ecol.* **25,** 36–47.

doi:10.1111/j.1442-9993.2009.02105.x