



Livestock grazing affects microclimate conditions for decomposition process through changes in vegetation structure in mountain grasslands



María Victoria Vaieretti^{a,*}, Sabrina Iamamoto^b, Natalia Pérez Harguindeguy^{a,b}, Ana María Cingolani^{a,b}

^a Instituto Multidisciplinario de Biología Vegetal, (CONICET-Universidad Nacional de Córdoba). CC 495, (5000), Córdoba, Argentina

^b Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Av. Vélez Sarsfield 299, (5000), Córdoba, Argentina

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ABSTRACT

It is often assumed that a change in litter quality is the main driver of alterations in the decomposition process when grazers modify vegetation structure. Soil microclimate is also modified, but this driver of decomposition has been far less studied than litter quality. We analyzed the relationships among vegetation structure, microclimate and decomposition in different mountain grassland types, across a fence-line separating paddocks with different grazing intensity. Along the fence, we selected nine pairs of contrasting grassland types including lawns and tall tussock grasslands, which are associated with high and low local grazing pressure, respectively. At each site (N = 18) we estimated growth form composition and vegetation height. During the growing season we recorded soil temperature, soil moisture and the photosynthetically active radiation. Within the same period, we measured the decomposition rate of two common litter substrates. We analyzed the relationships among those variables at the landscape and at the local scale. At the landscape scale we considered the variation across all sites (N = 18). At the local scale we considered each pair as a sample (N = 9) and the differences between both sides of the fence as the variables to correlate. Our results indicate that when short grasslands are released from grazing and tall grasslands became dominant, temperature and light at the soil level are reduced, while soil moisture tends to increase, enhancing decomposition. Furthermore, these results show that the microclimatic conditions effect can counteract the litter quality effect (reported in previous studies) on decomposition, resulting in increased decomposition rates when grazing is reduced.

1. Introduction

Mountain ecosystems are experiencing land-use changes in an unprecedented way. Pastoral practices have become the main economic activity in these ecosystems in response to the advancement of agriculture on lowlands (Asner et al., 2004). The potential consequences of grazing on litter decomposition through changes in plant biomass quantity and quality as well as dung and urine deposition is well established (Bardgett and Wardle, 2010; Olofsson and Oksanen, 2002; Olofsson et al., 2004; Semmartin et al., 2004, 2010). However, the impact of grazing on changes in soil microclimatic conditions (e.g. soil temperature and moisture) associated with changes in vegetation structure has received little attention, despite their potentially important effects on the decomposition process (Gass and Binkley, 2011; Risch et al., 2007; Stark et al., 2010). Some components of vegetation structure, as dominant growth forms and the quantity of green and standing dead biomass, determine the soil microclimatic conditions.

Grazing influences plant community structure and species composition. On the one hand, plant height is reduced by herbivore consumption of aboveground biomass, further leading to a more prostrate growth of dominant plants (Díaz et al., 2007). On the other hand, the consumption of aboveground tissues can promote a replacement of tall by short species, and if grazing persists, it prevents the recolonization of tall species. Vegetation height and aboveground biomass reduction can result in less transpirational surface and a greater soil exposure to radiation and weather elements in grazed areas. Accordingly, LeCain et al. (2000) found higher soil moisture in an ungrazed pasture compared to a grazed one, which was attributed to accumulated litter and standing dead biomass in the ungrazed site. Other authors reported that in woodland systems, grazers may remove the foliage and understory vegetation, leading to an increase in soil temperature concomitant with a decrease in soil moisture (Yates et al., 2000; Xiong et al., 2008). These changes in soil temperature and moisture regimes have important consequences for soil microbial processes by regulating microbial

* Corresponding author.

E-mail addresses: vaieretti@imbiv.unc.edu.ar (M.V. Vaieretti), sagomaia@gmail.com (S. Iamamoto), perez.h.natalia@gmail.com (N. Pérez Harguindeguy), acingola@yahoo.com.ar (A.M. Cingolani).

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activity (Klump et al., 2011; Olofsson et al., 2004; van der Waal et al., 2001). In general, high soil temperature combined with enough soil moisture availability enhance microbial activity, but it could be slowed down when soil moisture is limited (Almagro et al., 2009; Voroney, 2007). However, despite the importance of soil temperature and moisture to microbial activities, few studies have analyzed how the changes in vegetation structure induced by grazing could alter litter decomposition processes mediated by changes in soil microclimatic variables.

In the upper belt of the Córdoba mountains in central Argentina, livestock production has been the main economic activity since the beginning of the 17th century (Díaz et al., 1994). Through differential use, domestic herbivores maintain a mosaic of different grassland types including grazing lawns and open and closed tall tussock grasslands (Cingolani et al., 2003, 2010; 2014; Pucheta et al., 1998a). In this system, as in other grasslands, herbivores avoid tall vegetation and strongly select grazing lawns, preventing their conversion into tall tussock grasslands (Cingolani et al., 2003, 2014; Pucheta et al., 1998a, 1998b; von Müller et al., 2017). As predicted by classical theories on the impact of large herbivores in productive systems (Bardgett and Wardle, 2003; McNaughton, 1984; McNaughton et al., 1997; Pastor et al., 2006), selective grazing maintain a low input of high quality litter (and hence high decomposability) in lawns, while tussock grasslands receive a high input of low quality litter (Vaieretti et al., 2013). Lawns also receive an important input of dung (Vaieretti et al., 2010; von Müller et al., 2012, 2017), which could contribute to accelerated decomposition rates and nitrogen mineralization (Bardgett and Wardle, 2003). However, despite the differences in the quantity and quality of resources that enter into the soil, in a previous study we found that *in situ* litter decomposition rates were similar in lawns and in closed tussock grasslands, yet lower in open tussock grasslands (Vaieretti et al., 2013).

In that study, we found that *in situ* litter decomposition rates were explained mainly by the microenvironmental conditions (40% of variance, tested by the average of common substrates decomposition rate), while litter decomposability (i.e. decomposition due to litter quality, tested by the average of litter decomposition in a common garden) explained only 15% of variance (see also Poca et al., 2015). These results suggest that some aspects of the microenvironment (the combination of soil physicochemical and biological properties, and microclimate; Eviner and Chapin, 2003) may be the main drivers of field decomposition rates. Considering that in our previous studies (Vaieretti et al., 2010, 2013) soil physicochemical properties were similar across the different grassland types and were not related to differences in decomposition, we hypothesize that it is the microclimate which determine the soil environment effect on decomposition in the field. To test this hypothesis, we here attempted to answer the following questions: (1) How does vegetation structure, as a result of the grazing regime, affect microclimatic conditions? (2) How vegetation structure and microclimatic conditions affect decomposition?

2. Materials and methods

2.1. Study area

The study area is located in a high plateau of Córdoba mountains, in central Argentina (31° 37'S, 64° 48'W). Mean temperatures of the coldest and warmest month are 5.08 °C and 11.48 °C, respectively, with no frost-free period. Mean annual precipitation is 900 mm (1992–2010), mostly concentrated between October and April, which are the warmest months (Colladon et al., 2010). Soils are classified as mollisols, derived from the weathering of the granitic substrate and fine-textured eolian deposits (Cabido et al., 1987). The vegetation of the area is strongly determined by pastoral use and fire events, which in combination with topography result in different landscape units dominated by different plant growth forms (Cingolani et al., 2003, 2004, 2008).

The principal productive activity in the area is livestock raising, which is primarily focused on cattle (mainly Aberdeen Angus breed). Because of the large size of the paddocks, animals can select among different landforms and plant communities (von Müller et al., 2017). At 2000 m s. n.m. three main distinct grassland types can be visually identified: short lawns, open tussock grasslands and closed tussock grasslands. These grassland types are maintained by different local grazing pressure (Cingolani et al., 2003, 2014; Vaieretti et al., 2010, 2013).

Lawns are mainly dominated by annual and perennial grasses and forbs which are highly consumed by herbivores because of their high foliar nutrient content (Pérez Harguindeguy et al., 2000; Pucheta et al., 1998a; Vendramini et al., 2000). These patches have high plant alpha diversity and are associated to high local grazing pressure (Cingolani et al., 2010; Vaieretti et al., 2013; von Müller et al., 2017). Open tussock grasslands comprise a mixture of short plants and tussock species (Cingolani et al., 2003; Pucheta et al., 1998a; Vaieretti et al., 2010). These grasslands in general are dominated by thin tussock grasses such as *Deyeuxia hieronymi* (Hack.) Turpe and several species of *Festuca*, but also present high cover of graminoids and forbs as *Carex* spp. and *Lachemilla pinnata* (Ruiz & Pav.) Rothm. (Vaieretti et al., 2010). Open tussock grasslands are usually associated with high or moderate local grazing pressure (Vaieretti et al., 2013; von Müller et al., 2017). Closed tussock grasslands are strongly dominated by tall tussocks of *Poa stuckertii* (Hack.) Parodi, and other species. This type of grassland is associated to very low or no local grazing pressure (Vaieretti et al., 2013; von Müller et al., 2017). The study was performed in the Quebrada del Condorito National Park and an adjacent area under private ownership. In the section of the National Park selected for this study, livestock was maintained in an attempt to prevent the loss of plant diversity and the excessive accumulation of biomass, which can lead to wildfires (von Müller et al., 2017).

2.2. Experimental design

We selected two adjacent fenced paddocks under different grazing regimes (sustained for at least 15 years). The paddock in the National Park was under continuous stocking density of 0.13 Cattle Equivalents per ha (CE ha⁻¹), which represents low cattle pressure for this grassland system (Cingolani et al., 2014; von Müller et al., 2017), and was characterized by a matrix of closed and open tussock grasslands with some patches of grazing lawns, besides other cover types. The paddock under private ownership was under an average annual stocking density of 0.20 EC. ha⁻¹ which represents high cattle pressure, and the vegetation was characterized by a matrix of grazing lawns with some patches of tussocks grasslands, besides other cover types (see Supplementary Material; file S1). We selected nine pairs of sampling sites of contrasting grassland types along the fence. Sites had an area of approximately 100 m². The pairs of sampling sites were located at distances of at least 25–30 m to each other (see Supplementary Material; file S1). Two pairs of sites were lawns contrasted with open tussock grasslands, two pairs were lawns contrasted with closed tussock grasslands, and two pairs were open tussock grasslands contrasted with closed tussock grasslands. In all pairs, the site with more open vegetation was located in the high grazing paddock (i.e. the private ownership paddock; Table 1). Additionally, we selected three pairs of sites conformed by the same grassland type at each side of the fence (one pair of each grassland type) which were used as controls (Table 1). The distance among sites of the same pair separated by the fence varied between one and two meters. All pairs of sampling sites were located at similar altitudes (2140–2160 m a.s.l.), at gentle slopes (2–10%) with south-west aspect and slightly variable topographic positions. The fence-line provide a direct comparison, at both sides of each pair, of vegetation structure due to differences in past and present grazing management avoiding differences in topography or pre-existent soil characteristics. Designs like this have been used to analyze the effect of

Table 1

Paired sites selected along the fence-line, describing the patch types located at each side of the fence that separate the paddocks with different grazing intensity. TG = tussock grasslands.

Combinations of patch type	Sites N°	Private Ownership (high grazing paddock)	National Park (low grazing paddock)
Lawns – Open TG	1–2	Lawn	Open TG
	3–4	Lawn	Open TG
Lawns – Closed TG	5–6	Lawn	Closed TG
	7–8	Lawn	Closed TG
Open TG – Closed TG	9–10	Open TG	Closed TG
	11–12	Open TG	Closed TG
Controls	13–14	Lawn	Lawn
	15–16	Open TG	Open TG
	17–18	Closed TG	Closed TG

grazing on plant richness and diversity, seed production and plant traits, among other factors (Cingolani et al., 2005; Dorrrough et al., 2004; McDowell et al., 2004; Todd and Hoffman, 1999).

2.3. Vegetation structure

At each sampling site, at the beginning of the 2011 growth season, we selected a representative area of 16 m², delimited by stakes in its four corners (see Supplementary Material; file S1), where we visually estimated the cover (%) of different plant growth forms (forbs, perennial graminoids, annual graminoids, thick tussock grasses, thin tussock grasses, lichens, and mosses), together with litter and bare soil. Additionally, inside of the representative area we measured maximum vegetation height in 20 randomly placed 625 cm² quadrats and calculated the average height per site.

2.4. Microclimatic conditions

We measured microclimatic conditions during the 2011–2012 growing season, i.e. from December 2011 to March 2012 (90 days). At each site, we placed one iButton DS1921G-F5 (resolution of 0.5 °C) sensor at 0–5 cm depth to register soil temperature every three hours. For each site we calculated daily soil temperature averages which were used to obtain the average soil temperature for the entire growing season. We measured soil moisture of the upper horizon (0–5 cm) at each site by collecting a soil compound sample every 15 days. We determined soil water content through the gravimetric method (Jarrell et al., 1999). In the laboratory we weighed all soil samples (fresh weight), we dried them at 105 °C in the oven for 48 h, and then we re-weighed them (dry weight). We calculated soil water content (%) as the proportional weight lost. For each site we calculated the average of soil water content for the entire period. Simultaneously to the collection soil samples for soil moisture measurements, we recorded photosynthetically active radiation (PAR) at the soil level for each site with a Li-Cor LI-1400 sensor. For each site we obtained an average of PAR for the whole growing season.

2.5. Decomposition rates of common substrates

Decomposition rates were measured using common substrates through the standardized litter-bags technique (Pérez Harguindeguy et al., 2013). As common substrates we selected the litter of two abundant species in the study area: a native annual grass, *Muhlenbergia peruviana* (P Beauv.) Steud. and a native perennial grass, *Poa stueckertii* (Hack.) Parodi. For each species, we randomly collected and pooled the litter across the 18 sampling sites. We constructed 180 bags of 0.3 mm nylon mesh size for each species, filled with 1 g of air-dried substrate. We incubated the bags above the soil surface, below the litter layer (10 bags of each substrate per site), fixed to the ground with stakes and protected with barbed wire to avoid damage by cattle and small animals, during 2011–2012 growing season, i.e. from December 2011 to

March 2012 (90 days of incubation).

After the incubation period, the harvested bags were carefully cleaned removing adhering soil, soil fauna and other extraneous materials by brushing. We oven-dried all cleaned bags for at least 48 h at 60 °C, and then weighed them. To estimate initial dry mass before incubation, we calculated air-dried water content by drying sub-samples of substrates litter at 60 °C during 48 h. Water content (%) was calculated from the weight loss in sub-samples after drying. We estimated decomposition of each common substrate as the dry weight loss (%) at the end of the incubation period (Pérez Harguindeguy et al., 2013). We obtained one value of decomposition per site per substrate by averaging the dry weight loss of 10 litter bags.

2.6. Data analyses

We described the variation in vegetation structure across sites through Principal Component Analysis (PCA). We used the following variables: cover (%) of forbs, perennial graminoids, annual graminoids, thick tussock grasses, thin tussock grasses, lichens, mosses, litter and bare soil, and the average vegetation height (cm). Based on the results of this analysis, we selected short herbs (the sum of forbs, perennial graminoids and annual graminoids) and plant height as the most representative variables to describe vegetation structure. These variables were used in further analyses.

To analyze the relationships between vegetation structure and microclimatic variables, and their relationships with decomposition of common plant substrates, we performed Pearson correlation analysis at two levels. On the one hand, we performed a landscape level analysis considering each site as a sample for the correlations (N = 18). On the other hand, at the local level, we aimed to detect only variations related with different grazing management practices avoiding potential differences associated to topography. Therefore, we used each pair as a sample (N = 9), and the differences between both sides of the fence as the variables to correlate.

At the landscape level, i.e. considering the variation measured across all sites (N = 18), we correlated the cover of short herbs and vegetation height (as variables representative of vegetation structure) with the average soil temperature, soil moisture and PAR (as microclimatic variables). We also correlated plant structural variables and microclimatic variables with decomposition of both plant substrates.

At the local level, we analyzed how the differences in microclimate and vegetation structure between sites of the same pair are related among them and with differences in decomposition. We performed correlation analysis across the pairs of sampling sites (N = 9). To carry on this analysis, we calculated the differences of vegetation structure and microclimatic variables, and also decomposition rates between sites of the same pair, as follows:

$$X_{dif} = X_{PO} - X_{NP}$$

where X_{PO} is the value of the variable X for the site located in high grazing paddock (private ownership), X_{NP} is the value of variable X for the site located in low grazing paddock (National Park), and X_{dif} is the difference between both values. Based on these calculations, we obtained new variables for the nine pairs of sampling sites: difference in common substrate decomposition rate; difference in short herbs cover; difference in vegetation height; difference in soil temperature; difference in soil moisture and difference in PAR. It is important to note that when the value of the focal variable was higher in the low grazing paddock than in the high grazing paddock, the difference was negative.

3. Results

3.1. Vegetation structure

The three grassland types were well separated along Axis 1 (explaining 42.6% of the variance), which was associated with dominance

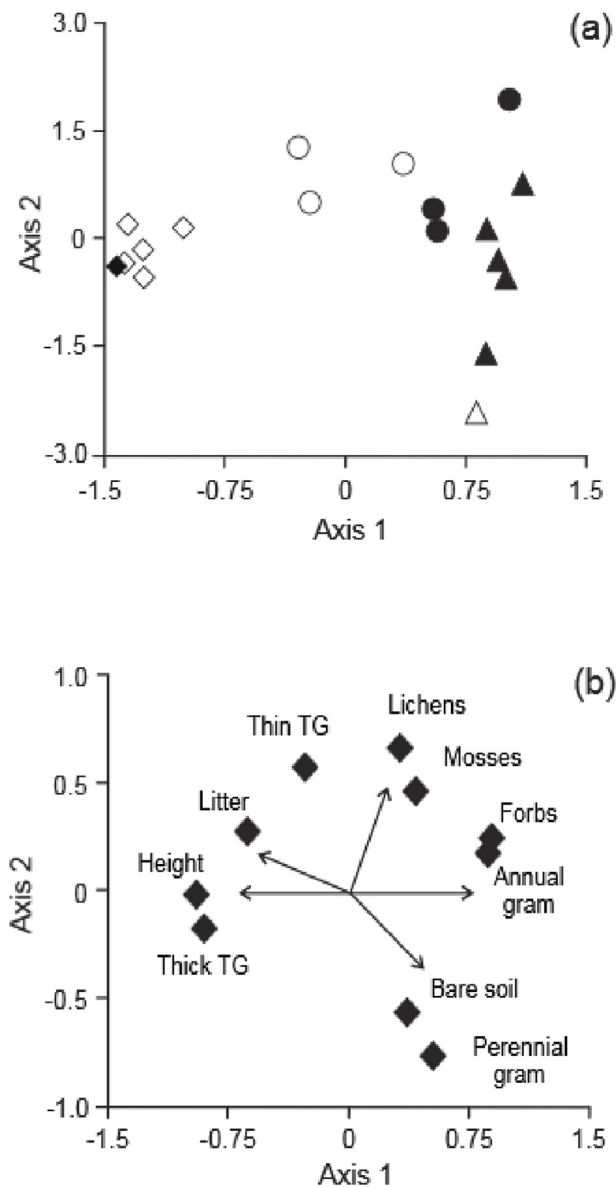


Fig. 1. Diagrams of Principal Component Analysis (PCA) ordination of the 18 selected sites (a), and contribution of different vegetation structure variables (b). Filled symbols denote sites located in the high grazing paddock (private ownership) and open symbols denote sites located in low grazing paddock (National Park): lawns; open tussock grasslands and: closed tussock grasslands. TG = Tussock grasses; gram = graminoids.

of short herbaceous species (forbs, perennial and annual graminoids) in the positive side, and dominance of tall tussock grasses in the negative side (Fig. 1a and b). Axis 2 (explaining 21.2% of the variance) separated sites with highest bare soil and annual grass cover to the negative side from those with highest lichen and moss cover to the positive side (Fig. 1a and b). Based on correlation analysis between the vegetation variables (or combinations of variables) and the first Axis, we selected the two variables which summarized vegetation structure: cover of short herbs (i.e.: sum of forbs, perennial and annual graminoids cover, $r = 0.96$; $P < 0.0001$), and vegetation height ($r = -0.95$; $P < 0.0001$).

3.2. Relationships between vegetation structure and microclimate

At the landscape level (N = 18) sites with tall vegetation and low cover of short herbaceous plants had colder soils, received less light at

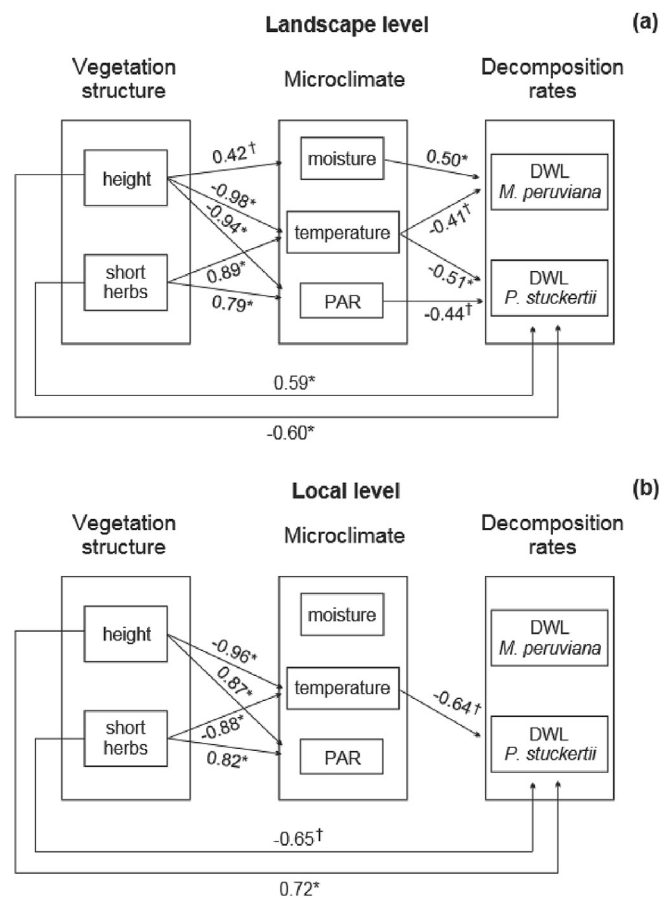


Fig. 2. Pearson correlations among vegetation structure (vegetation height and percentage of cover of short herbs), microclimate (soil temperature, soil moisture and photosynthetically active radiation-PAR) and decomposition rate (DWL = dry weight loss of common materials (%), *Muhlenbergia peruviana* and *Poa stuckertii*), (a) at the landscape level (N = 18), and (b) at the local level (N = 9). Significant ($P \leq 0.05$, indicated with an asterisk (*)) and marginally significant ($P \leq 0.1$, indicated with a cross (†)) correlations are represented with arrows. Pearson correlation coefficients (r) are indicated in both cases.

the soil surface, and tended to have higher soil moisture (Fig. 2a). At the local level (N = 9), relationships among vegetation structure and microclimate were similar to those at the landscape level. Sites with tall vegetation and low cover of short plants were colder and more shady than adjacent sites (i.e. at the other side of the fence) with the opposite vegetation characteristics (Fig. 2b). However, at this level of analysis, we did not find significant nor marginally significant relationships between differences in vegetation structure and differences in soil moisture (Fig. 2b).

3.3. Relationships between vegetation structure, microclimate and decomposition

Both plant common substrates presented similar decomposition patterns across all sampling sites ($r = 0.60$; $P = 0.008$; $N = 18$). Dry weight loss ranged from 24 to 40% for *M. peruviana*, and 15–30% for *P. stuckertii*.

At the landscape level (N = 18), decomposition of *M. peruviana* was higher in sites with higher soil moisture, which tended to be colder (Figs. 2a and 3a), but it was not related to vegetation structure. Decomposition of *P. stuckertii* was also higher in sites with colder soils, which tended to be shadier (Figs. 2a and 3b), but it was not associated with soil moisture. Furthermore, decomposition of *P. stuckertii* was higher in sites with tall vegetation (Figs. 2a and 4a) and low cover of short herbs (Figs. 2a and 4b).

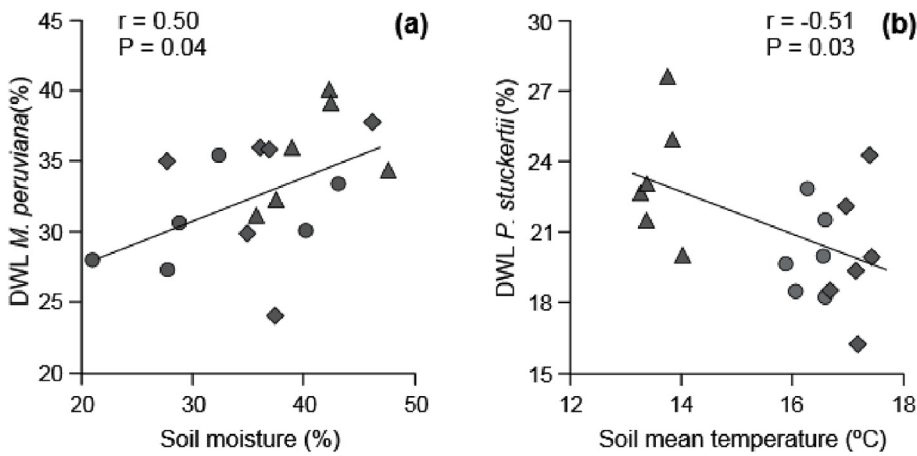


Fig. 3. Relationships between, (a) decomposition (DWL = dry weight loss (%)) of *M. peruviana* and soil moisture (%); and (b) decomposition (DWL%) of *Poa stueckertii* and soil temperature (°C), at landscape level (N = 18). Represent lawns; represent open tussock grasslands, and represent closed tussock grasslands. r = Pearson correlation coefficient; P = level of significance. A solid line graphically representing the slope of the relationship was drawn for illustrative purposes.

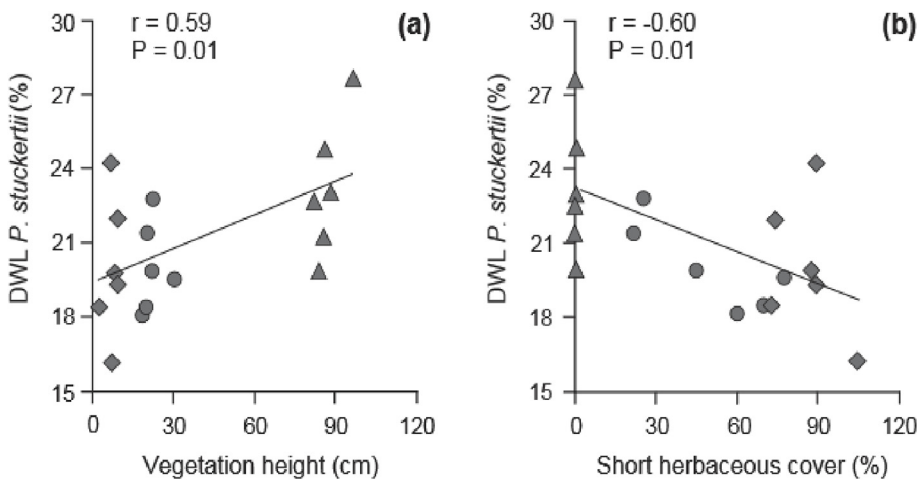


Fig. 4. Relationships between decomposition of *Poa stueckertii* (DWL = dry weight loss (%)) and vegetation structure at landscape level (N = 18): (a) vegetation height (cm), (b) short herbaceous cover (%). Represent lawns; represent open tussock grasslands and represent closed tussock grasslands. r = Pearson correlation coefficient; P = level of significance. A solid line graphically representing the slope of the relationship was drawn for illustrative purposes.

At the local level (N = 9), differences in decomposition of *M. peruviana* were not associated with differences in either microclimate or vegetation structural characteristics (Fig. 2b). Nonetheless, and consistently with the pattern found at the landscape level, *P. stueckertii* decomposed faster in sites with taller vegetation that tended to have colder soils (Figs. 2b and 5), compared to warmer adjacent sites with shorter vegetation.

4. Discussion

Our results provide important insights on the relationships between vegetation structure (associated to different grazing pressure), microclimate and the decomposition process in the mountain grasslands under study. Our results suggest that when a short grassland is released from grazing (i.e. by excluding or reducing livestock stocking rate), and tussock grasslands became dominant, temperature and light at soil level decrease, while decomposition is enhanced. Similar relationships among some components of vegetation structure, soil microclimate and microbial activity have been observed in other grassland systems, and even in forest systems. Risch et al. (2007), in grasslands of Yellowstone National Park, found that soil moisture was positively correlated with decomposition of a common substrate, while soil temperature was negatively correlated. Also Stark et al. (2010), in forests of Finland, found that higher soil temperatures in grazed sites did not accelerate decomposition rates in relation to ungrazed sites. In addition, they found higher soil moisture in ungrazed sites, which was attributed to a thick layer of lichen dead biomass.

Our results also indicate that a colder microenvironment could be better for decomposition than a warmer microenvironment. When plant

biomass (both standing and litter) is reduced, for example by grazing, the litter-soil interface where decomposition occurs get directly exposed to solar radiation, which could increase soil temperature, but also increases soil water losses through evaporation, and produce dehydration of the decomposing litter (Risch et al., 2007; Yates et al., 2000). In contrast, the shading effect of vegetation can decrease soil temperature and protect the soil and litter from water losses, creating a moister environment for decomposers (Suseela et al., 2014; Xiong et al., 2008). On this basis, we interpret that in our study area, the colder microenvironment under tussocks accelerates decomposition process by providing more optimum moisture levels at litter-soil interface, which promotes microbial activity. This interpretation was supported by the significant negative relationship, at the landscape level, between soil temperature and soil moisture ($r = -0.47$; $P = 0.05$; $N = 18$), as was either reported by Risch et al. (2007); but not by the relationship at the local level, which was not significant. The mechanism proposed above was neither fully supported by the relationships between decomposition and soil moisture, as we only found significant correlations at the landscape level and for one of the plant substrates used (*M. peruviana*). It is possible that decomposition is more directly promoted by the water content of the litter layer and the litter within the litter-bags (not measured in this study) than by the moisture content of the soil below them (de Santo et al., 1993). In other words, the higher temperatures of grazing lawns may be causing a greater impact on litter and litter-bag moisture (not completely reflected in soil moisture as we have measured it) determining a lower decomposition on those grassland types (Suseela et al., 2014).

Providing further support to this conclusion, our findings demonstrate that vegetation structural characteristics are strongly related with

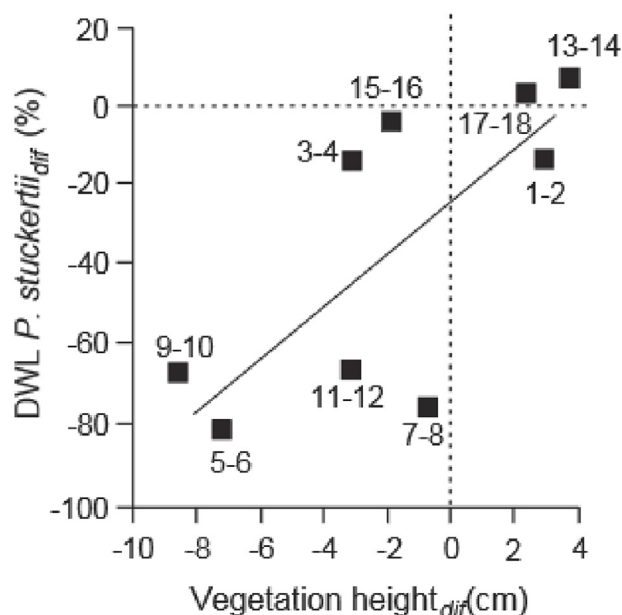


Fig. 5. Relationships between decomposition of *Poa stueckertii* (DWL = dry weight loss (%)) and vegetation height (cm) at local level (N = 9). The figure shows the differences of *Poa stueckertii* decomposition (between the sites of the same pair) against the differences in vegetation height. The calculations of the differences always were performed subtracting the variable values of the sites located in the high grazing paddock to the variable values of the sites located in the low grazing paddock. Points are labelled with two numbers which represent the sites (see Table 1). *diff* = difference; $r = 0.72$, $P = 0.03$ (Pearson correlation coefficient and level of significance, respectively). A solid line graphically representing the slope of the relationship was drawn for illustrative purposes.

decomposition rates of *P. stueckertii*, both at the landscape and the local levels (i.e., decomposition was faster in sites with taller vegetation and low cover of short herbaceous plants). Previous studies in the area have demonstrated that live and dead standing biomass are directly related with the accumulated litter across the different grasslands types (Pucheta et al., 1998a; Vaieretti et al., 2013). The combination of tall vegetation with high accumulated litter probably provides further protection to the soil-litter interface and the litter-bags from desiccation not only by cooling the microenvironment but also by protecting moisture from the air circulation. Additionally, tall vegetation and litter act buffering the microenvironmental variability in temperature and moisture (Supplementary Material; files S2 and S3). This more stable microclimate may promote a more constant microbial activity, resulting in higher decomposition rates in tussock grasslands respective to grazing lawns (LeCain et al., 2000; Lee et al., 2014; Xiong et al., 2008). Further studies through controlled experiments, as reported by Xiong et al. (2008), may elucidate how vegetation structure affects litter moisture.

It is important to note that we found a different decomposition pattern than in our previous study (Vaieretti et al., 2013; where we found that the decomposition rates of common substrates were similar in grazing lawns and in closed tussock grasslands). This discrepancy between studies is probably related to the location of the sampling sites of these two studies in different positions along the topographic gradients within the study area. The study sites selected by Vaieretti et al. (2013) were located at lower topographic positions with more humid soils compared to sites selected for the present study, which were located at upper topographic positions with drier soils. Therefore lawns analyzed in the previous study could be classified as mesic-wet lawns, while those of the present study could be classified as mesic-xeric (*sensu* Cingolani et al., 2003). Accordingly, in the lawns selected before (Vaieretti et al., 2013), soil moisture values were high during all the experiment and litter may have never been dry enough to produce a

decrease in microbial activity, resulting in similar decomposition rates than tussock grasslands, despite the direct soil radiation and probably high temperature. In the present study, lawns were more xeric and, because of that, the water content of the litter may have been more susceptible to high temperature and to direct evaporation, resulting in lower decomposition rates in relation to tussock grasslands. Similarly, Risch et al. (2007) found that high soil temperature decreased the soil moisture in driest hill-top soils, while temperature did not affect soil moisture in slope-bottom soils.

In addition, the slight variations in topography along our study pairs may also be the cause of the differences between the patterns found at the landscape and at the local levels. In this sense, although the dynamic of soil temperature were similar between sites of the same grassland type, the dynamic of soil moisture in most cases was different between sites of the same grassland type. These patterns can be observed in the control pairs (i.e. pairs of sites of same grassland type at each side of the fence; see Supplementary Material; files S3d). The microtopographic differences between grassland types of the same pair could be the causes of different patterns of soil water accumulation or runoff that could alter the patterns of soil moisture, and particularly influence the pattern at local level.

5. Conclusions

The results of our study highlight the importance of considering the effect of large herbivores on soil processes not only through the changes in litter biomass and quality, but also via the impact of vegetation structure on microenvironmental conditions (Gass and Binkley, 2011). Our present results, combined with our previous results (Vaieretti et al., 2013) and those of Poca et al. (2015), suggest that vegetation regulate decomposition through its influence on soil and litter temperature and moisture more than through litter quality. Moreover, in the present study the effect of microclimate was opposite to the effect of litter quality (Vaieretti et al., 2013). The patterns obtained here could be operating in other grassland systems, and should be considered when evaluating the role of grazers on ecosystem processes.

Author contributions

MVV, NPH and AMC conceived the ideas, MVV and SI conducted the field and laboratory work, MVV and AMC conducted the statistical analyses. MVV, NPH and AMC wrote the manuscript.

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