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Combined effects of leaf litter and soil microsite on decomposition process in arid rangelands

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ABSTRACT

The objective of this study was to analyze the combined effects of leaf litter quality and soil properties on litter decomposition and soil nitrogen (N) mineralization at conserved (C) and disturbed by sheep grazing (D) vegetation states in arid rangelands of the Patagonian Monte. It was hypothesized that spatial differences in soil inorganic-N levels have larger impact on decomposition processes of non-recalcitrant than recalcitrant leaf litter (low and high concentration of secondary compounds, respectively). Leaf litter and upper soil were extracted from modal size plant patches (patch microsite) and the associated inter-patch area (inter-patch microsite) in C and D. Leaf litter was pooled per vegetation state and soil was pooled combining vegetation state and microsite. Concentrations of N and secondary compounds in leaf litter and total and inorganic-N in soil were assessed at each pooled sample. Leaf litter decay and soil N mineralization at microsities of C and D were estimated in 160 microcosms incubated at field capacity (16 month). C soils had higher total N than D soils (0.58 and 0.41 mg/g, respectively). Patch soil of C and inter-patch soil of D exhibited the highest values of inorganic-N (8.8 and 8.4 $\mu\text{g/g}$, respectively). Leaf litter of C was less recalcitrant and decomposed faster than that of D. Non-recalcitrant leaf litter decay and induced soil N mineralization had larger variation among microsities (coefficients of variation = 25 and 41%, respectively) than recalcitrant leaf litter (coefficients of variation = 12 and 32%, respectively). Changes in the canopy structure induced by grazing disturbance increased leaf litter recalcitrance, and reduced litter decay and soil N mineralization, independently of soil N levels. This highlights the importance of the combined effects of soil and leaf litter properties on N cycling probably with consequences for vegetation reestablishment and dynamics, rangeland resistance and resilience with implications for management and conservation.

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1. Introduction

A substantial fraction of the annual net primary production senesces and enters to the decomposition subsystem in most terrestrial ecosystems (McNaughton et al., 1989). Plant litter decomposition and mineralization are important processes for ecosystem functioning regulating nutrient availability and carbon cycling (Lambers et al., 2000). The rates of these processes depend on climate, quality and composition of litter mixtures, and soil biotic and abiotic components (Ald, 2003).

In most arid and semiarid ecosystems vegetation displays a patchy structure consisting of dense plant patches dominated by

shrubs and perennial grasses distributed on a matrix of scattered vegetation or bare soil (Whitford, 2002). Both life forms differ in structural and physiological traits and in mechanisms of N conservation contributing with different amount and quality of leaf litterfall (Aerts and Chapin, 2000; Campanella and Bertiller, 2008; Carrera et al., 2009). Shrubs with long-lasting leaves and low leaf N resorption rates produce recalcitrant leaf litter with high concentration of secondary compounds such as lignin and soluble phenolics (Aerts and Chapin, 2000; Carrera and Bertiller, 2010; Carrera et al., 2009; Moreno et al., 2010). In contrast, perennial grasses with short lived leaves, produce non-recalcitrant leaf litter with low concentration of secondary compounds (Aerts and Chapin, 2000; Campanella and Bertiller, 2008; Carrera et al., 2005). High concentrations of secondary compounds may reduce litter decomposability by either toxic effects on microorganisms or by retarding microbial breakdown of organic matter (Lambers et al., 2000). Accordingly, some plant chemical traits reflecting

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physiological and biochemical adaptations to the environment could be used as predictors of rates of litter decomposition and nutrient release (Lambers et al., 2000; Xu and Hirata, 2005). However, in litter mixtures, chemical properties of single species could have strong effects on decomposition and nutrient release enhancing or retarding the rates expected by the relative contribution of individual species to litter mixtures (Gartner and Cardon, 2004; Pérez-Harguindeguy et al., 2000; Wardle, 2002).

Arid and semiarid ecosystems are usually grazed by domestic herbivores at low stocking rates (Reynolds et al., 1997). Selective grazing reduces plant cover of preferred species and induces the replacement of herbaceous plants by long-lived evergreen woody plants with slow growth rates (Bertiller and Ares, 2011; Bertiller and Bisigato, 1998; Schlesinger et al., 1996). This in turn, leads to increasing contribution of shrubs to leaf litterfall and recalcitrance of leaf litter mixtures (Carrera et al., 2008, 2009). Accordingly, grazing could indirectly affect the input and output fluxes to soil organic matter (Milchunas and Lauenroth, 1993). Moreover, grazers could also have direct effects on soil properties increasing bulk density by trampling or increasing labile N concentration through urine and faeces inputs (Prieto et al., 2011; Steffens et al., 2008). The combined effects of changes in soil and litter mixture properties induced by grazers may affect the metabolic functioning of soil microorganism communities thus controlling the rates of leaf litter decomposition and nutrient release in grazed ecosystems (Carrera et al., 2009; Li et al., 2011; Pucheta et al., 2004; Whitford, 2002). Since both animal depositions and leaf litterfall are not homogeneously spatially distributed, different combinations of soil and litter properties could induce small spatial differences in soil resource levels which could differentially affect plant processes (Luzuriaga and Escudero, 2008). This is an important issue related to processes leading to plant recovery (i.e. emergence, establishment, growth) and to ecosystem resistance and resilience (Gregory et al., 2009) that has been scarcely explored in grazed ecosystems. The objective of this study was to evaluate the combined effects of leaf litter quality and soil properties on leaf litter decomposition rates and soil potential N mineralization in conserved and disturbed by grazing vegetation states in arid rangelands of the Patagonian Monte. It was hypothesized that spatial differences in soil inorganic-N levels have larger impact on decomposition processes of non-recalcitrant than recalcitrant leaf litter (low and high concentration of secondary compounds, respectively). It was predicted that leaf litter from conserved vegetation states would be less recalcitrant and its decomposition rates and N mineralization in the associated soil would have larger variation among soil microsites differing in the levels of inorganic-N than leaf litter from disturbed by grazing vegetation states.

2. Materials and methods

2.1. Study area

The study was carried out in the southern portion of the Monte Phytogeographic Province (Patagonian Monte), Argentina (42° 39'S, 65° 23'W, 115 m a.s.l.). The mean annual temperature is 13.7 °C and the mean annual precipitation is 235.9 mm (22-year average, Centro Nacional Patagónico, 2009). Soils are a complex of Typic Petrocalcids- Typic Haplocalcids (del Valle, 1998; Soil Survey Staff, 1998). Vegetation corresponds to the shrubland of *Larrea divaricata* Cav. and *Stipa* spp. (Soriano, 1950). Plant canopy covers less than 40% of the soil and presents a random patchy structure (Bisigato and Bertiller, 1997; Mazzarino et al., 1998). These ecosystems have been grazed by sheep since the beginning of the last century with a historical stocking rate of ca. 0.10–0.14 sheep/ha (Ares et al., 1990; Bertiller et al., 2002). The study was carried out on

an area of 2500 ha corresponding to a floristically homogeneous vegetation stand submitted to continuous grazing all year round with a stocking rate of ca. 0.14 sheep/ha (Bertiller et al., 2002). Within the area, two sites ca. 2.5 h each were selected. One of them corresponded to a site excluded from domestic herbivores since 1993. The other was a grazed site with signs of high grazing disturbance adjacent to the site excluded from grazing. The selection of this latter was based on sheep fecal counts (Bisigato and Bertiller, 1997), perennial grasses cover (Bertiller and Bisigato, 1998; Carrera et al., 2008; Larreguy et al., 2012), soil indicators (Mazzarino et al., 1998), and remote sensing analyses (Ares et al., 2003). Disturbance by sheep grazing led to plant cover reduction, species substitution within the same plant life form, and plant life form replacement, especially perennial grasses by evergreen shrubs (Bertiller and Ares, 2008; Bertiller and Bisigato, 1998; Bertiller et al., 2002; Bisigato and Bertiller, 1997; Carrera et al., 2008) as well as to reductions in soil N fertility (Carrera et al., 2008). Both sites are representative of conserved (C) and disturbed by grazing (D) vegetation states (*sensu* Westoby et al., 1989) of the Patagonian Monte (Bertiller et al., 2002; Bisigato and Bertiller, 1997). In terms of reversibility of vegetation dynamics and ecological thresholds, D could be considered as an overgrazed site (Bertiller and Bisigato, 1998; Milchunas, 2006; Westoby et al., 1989). Both vegetation sites differed in canopy traits. Total, shrub, and grass covers were significantly higher at C (24.8, 18.8, and 5.8%, respectively) than D (13.7, 12.7, and 0.9%, respectively), but the relative cover of shrubs was significantly higher at D than C. The floristic list was highly similar between C and D (21 species and 22 species, respectively) with nineteen species in common (Table 1) but the relative dominance of shrub and perennial grass species changed between C and D. All perennial grass species had lower cover at D than at C. *Nassella tenuis* was the dominant perennial grass at C while *Pappostipa speciosa* dominated at D. Twelve shrub species had lower cover at D than at C. Six shrub species (*Chuquiraga avellaneadae*, *Chuquiraga erinacea*, *Junellia seriphoides*, *Larrea nitida*, *Prosopis alpataco* and *Schinus johnstonii*) and one perennial herb (*Aster haplopappus*) had higher cover at D than at C, but this increase did not compensate the decrease in cover of the other shrub species (Carrera et al., 2008). Both vegetation states had leguminous species (three at C and two at D), however C had higher cover of leguminous species than D (2.7 and 0.1%, respectively, Table 1).

2.2. Litterbag decomposition experiment and chemistry of leaf litter and soil

Sixty microsites were randomly selected within each vegetation state, a half of them (30) corresponded to plant patches of modal size (1.8–2.4 m diameter) and the other half (30) to the associated inter-patch areas of bare soil ca. 1 m diameter (Bisigato and Bertiller, 1997; Prieto et al., 2011). This sampling defined four microsite types with different characteristics: microsite 1 and 3 (patch microsites in C and D, respectively) and microsites 2 and 4 (inter-patch microsites in C and D, respectively).

Leaf litter accumulated on the soil was collected in plots of 0.50 × 0.25 m at each microsite during the period March–June 2008. Leaf litter was cleaned of attached soil particles, pooled per vegetation state (two pooled litter types: litter of C and litter of D) and dried at 45 °C for 48 h. Simultaneously, the upper 2 cm of soil was extracted with a metallic tube (2 cm height and 10 cm in diameter) at the center of the plot at each microsite. Soil samples were air-dried, sieved to 2 mm and pooled per microsite (four pooled soil samples, one per microsite). One hundred and sixty microcosms were constructed by filling glass flasks (6 cm diameter, 13 cm height) with 100 g of air-dried soil of each microsite (40 microcosms per microsite). A litterbag (5 cm diameter, 0.3 mm

Table 1
Plant life forms and species cover (%) at conserved (C) and disturbed by grazing (D) vegetation states (Carrera et al., 2008).

Plant life form – species	C	D
Evergreen tall shrubs		
- <i>Atriplex lampa</i> (Moq.) D. Diet.	1.25	0.73
- <i>Chuquiraga avellanadae</i> Lorentz		1.27
- <i>Chuquiraga erinacea</i> var. <i>hystrix</i> D. Don	2.37	2.97
- <i>Junellia alatocarpa</i> (Tronc.) Moldenke	1.43	0.05
- <i>Larrea divaricata</i> Cav.	2.11	0.88
- <i>Larrea nitida</i> Cav.	0.01	0.23
- <i>Schinus johnstonii</i> Barkley	0.07	0.18
Total	7.24	6.31
Deciduous shrubs		
- <i>Bougainvillea spinosa</i> (Cav.) Heimerl	0.15	0.05
- <i>Lycium chilense</i> Mier ex Bertero	0.18	0.10
- <i>Prosopidastrum globosum</i> (Gillies ex Hook. & Arn.) Burkart ^a	2.63	
- <i>Prosopis alpacato</i> Phil. ^a		0.12
Total	2.96	0.27
Dwarf shrubs		
- <i>Acantholippia seriphioides</i> (A Gray) Moldenke	1.36	0.38
- <i>Junellia seriphioides</i> (Gillies & Hook.) Moldenke	0.09	0.12
- <i>Nassauvia fuegiana</i> (Speg.) Cabrera	7.03	5.60
- <i>Tetraglochin caespitosum</i> Phil.	0.14	0.01
Total	8.62	6.11
Perennial herbs		
- <i>Aster haplopappus</i> (Remy) Kuntze		0.03
- <i>Baccharis melanopotamica</i> Speg.	0.10	0.09
- <i>Hoffmannseggia erecta</i> Phil. ^a	0.04	0.02
- <i>Hoffmannseggia trifoliata</i> Cav. ^a	0.01	
Total	0.15	0.14
Perennial grasses		
- <i>Elymus erianthus</i> Phil.	0.23	0.01
- <i>Nassella tenuis</i> (Phil.) Barkworth	3.33	0.07
- <i>Poa lanuginosa</i> Poir.	0.33	0.23
- <i>Poa ligularis</i> Nees ap. Steud.	0.92	0.24
- <i>Pappostipa speciosa</i> (Trin. & Rupr.) Peñailillo	0.99	0.32
Total	5.80	0.87

^a Leguminous species.

mesh) containing 1 g of leaf litter was placed on the top of the soil of each microsite: 20 litterbags with leaf litter of C and 20 litterbags with leaf litter of D. Each microcosm was watered at field capacity (15% soil moisture), and covered with a perforated film to reduce humidity losses while allowing gaseous exchange. All microcosms were incubated under constant temperature (25 °C) in a climatic chamber during 16 month. The soil moisture at each microcosm was maintained at field capacity by daily watering the soil along flask borders thus allowing a homogeneously humectation of litterbags in contact to the soil during incubation. After 3, 6, 11 and 16 month from the beginning of the incubation period, 5 microcosms per date, litter type and microsite were randomly removed from the flasks, cleaned from soil particles attached to them, dried at 45 °C during 48 h and weighed to assess the litter mass loss at each microcosm. The concentrations of N, soluble phenolics, and lignin in leaf litter were assessed by semi-micro Kjeldahl (Coombs et al., 1985), the Folin-Ciocalteu method with tannic acid as standard (Waterman and Mole, 1994), and the acid-detergent digestion technique (van Soest, 1963), respectively, in five sub-samples of each pooled leaf litter at the beginning of the assay.

Inorganic N concentration was assessed in a soil subsample of each microcosm at the beginning and at the end of the incubation period. At each date, soil samples were extracted with 1 M KCl (1:5 sample: solution ratio) and analyzed for N–NH₄⁺ and N–NO₃⁻ by the indophenol-blue method using the 'Uremia kit' of Wiener Lab, and by copperised Cd reduction (Keeney and Nelson, 1982), respectively. The potential N mineralization at each microcosm was

calculated as the difference between inorganic N concentrations at the end and at the beginning of the incubation period. Inorganic-N and potential N mineralization were expressed according to oven-dried (105 °C) soil weight. The total N concentration was also assessed in five soil sub-samples of each microsite by semi-micro Kjeldahl (Bremmer and Mulvaney, 1982) and the relative initial inorganic N (inorganic-N per unit total soil N) was calculated as the ratio inorganic N/total soil N.

2.3. Statistical analyses

One-way ANOVA was used to test for significant differences in leaf litter chemistry between litter types (C and D). Two-way ANOVA was performed to analyze the differences in soil N (total, initial inorganic N, and relative initial inorganic N) among sites and microsites. In this analysis, vegetation state was included as main factor, and microsite as a nested factor within vegetation state. Three-way ANOVA was performed to analyze the differences in the potential N mineralization among sites, microsites and litter types. In this analysis, vegetation state was included as main factor, and microsite and leaf litter type as nested factors within vegetation state. In those cases in which assumptions of ANOVA were not met, variables were logarithmic transformed (Sokal and Rohlf, 1981). A double negative exponential model was used to assess decay rate of dry mass during the 16-month incubation period (Swift et al., 1979) as follows:

$$y = a_1 * \exp^{-(*k_1)} + a_2 * \exp^{-(*k_2)}$$

where y is the dry mass of leaf litter in litterbags at time t (month), a_1 and a_2 are the constants of the equation, and k_1 and k_2 are the decay rates for metabolic/labile and structural/recalcitrant fractions of leaf litter (Kemp et al., 2003). The significance of the differences in decay rates of leaf litter between leaf litter types and among microsites were evaluated by comparing the standard errors of each estimated k by Student t -test (Zar, 1986). The relationships among litter and soil variables were also evaluated by regression analysis. Unless otherwise noted, the level of significance throughout this study was $p \leq 0.05$. All statistical analyses were performed with SPSS 7.0 (Norusis, 1997).

3. Results

3.1. Leaf litter chemistry and N in soil microsites (total N, initial inorganic-N, and relative initial inorganic N)

Leaf litter of conserved vegetation states (C) had significant lower concentrations of N, soluble phenolics and lignin than that of disturbed by grazing vegetation states (D) (non-recalcitrant and recalcitrant leaf litter, respectively, Fig. 1). Total soil N differed among sites and microsites (nested ANOVA: $F_{1, 20} = 240.04$, $p < 0.001$; $F_{2, 20} = 32.35$, $p < 0.001$, respectively), being higher in the soil of plant patches and inter-patch areas at C (microsites 1 and 2, respectively) than at D microsites (microsites 3 and 4, respectively; Fig. 2a). The highest and the lowest values of total N were found in the soil of plant patches at C (microsite 1) and at the soil of inter-patches of D (microsite 4), respectively (Fig. 2a). Initial inorganic N in soil varied among sites and microsites (nested ANOVA: $F_{1, 20} = 44.54$, $p < 0.001$; $F_{2, 20} = 125.09$, $p < 0.001$, respectively), and the highest values were found in soil of microsites 1 and 4 (Fig. 2b). The relative initial inorganic N (inorganic-N per unit total soil N) differed between sites and microsites (nested ANOVA: $F_{1, 20} = 154.33$, $p < 0.001$; $F_{2, 20} = 143.73$, $p < 0.001$, respectively), and the highest and the lowest values were found in the soil of microsite 4 and 2, respectively (Fig. 2c).

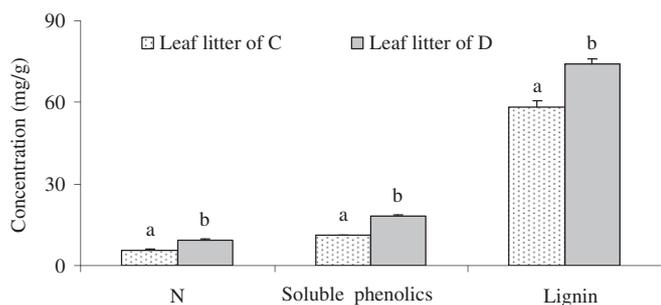


Fig. 1. Mean values of N, soluble phenolics and lignin concentrations in leaf litter of conserved (C) and disturbed by grazing (D) vegetation states (non-recalcitrant and recalcitrant leaf litter, respectively). Vertical lines indicate one standard error. Different lowercase letters indicate significant differences between both leaf litter types ($p < 0.05$).

3.2. Leaf litter decay and soil potential N mineralization

Mass decay rates of metabolic fractions (k_1) of non-recalcitrant leaf litter varied depending on the soil microsites (coefficient of variation = 25%, Fig. 3). The highest values of k_1 occurred in microsite 1 and microsite 4, while the lowest value of k_1 occurred in microsite 2 (Fig. 3). In contrast, mass decay rates of metabolic fractions (k_1) of recalcitrant leaf litter did not vary significantly among microsites (Fig. 3, coefficient of variation = 12%). Mass decay rate of recalcitrant fractions (k_2) of leaf litter were 2–3 order of magnitude lower than k_1 ($F_{1,8} = 47.10$, $p < 0.001$) and did not vary among litter types and microsites ($F_{1,8} = 0.05$, $p = 0.83$, $F_{1,8} = 0.05$, $p < 0.89$, respectively; Fig. 3). Soil potential N mineralization varied among sites, microsites, and leaf litter types (nested ANOVA: $F_{1,40} = 55.35$, $p < 0.001$; $F_{2,40} = 90.58$, $p < 0.001$; $F_{2,40} = 13.07$, $p < 0.001$, respectively; Table 2). The highest value of potential N mineralization was found in the soil of microsite 1 with leaf litter of C and the lowest in the soil of microsite 4 with litter of D (Table 2). The variation in soil potential N mineralization among microsites was larger with C than with D leaf litter (coefficient of variation = 41 and 32%, respectively).

3.3. Relationship between decomposition rate of metabolic fraction (k_1) of leaf litter and soil N

Decomposition rates of non-recalcitrant leaf litter (C) were higher than those of recalcitrant litter (D) in all microsites but in both cases they were not related to the level of total soil N (Fig. 4a). However, the variation in decay rates of non-recalcitrant litter was associated with the level of initial inorganic N (Fig. 4b) and relative inorganic N (Fig. 4c). Total soil N (positively correlated) and remaining dry mass (negatively correlated) explained the variation in potential N mineralization in the soil under non-recalcitrant leaf litter among microsites (Table 3). Total soil N was the only variable (positively correlated) explaining the variation in potential N mineralization in the soil under recalcitrant leaf litter among microsites (Table 3).

4. Discussion

Disturbances affecting litter and soil properties could play essential roles in the dynamic of soil microorganisms, nutrient cycling and consequently in plant processes (Wardle, 2002). Observed differences in leaf litter quality between conserved and disturbed vegetation states could be associated with increasing abundance of shrubs with well-defended leaves in plant canopies disturbed by grazing as was reported in the study area (Campanella

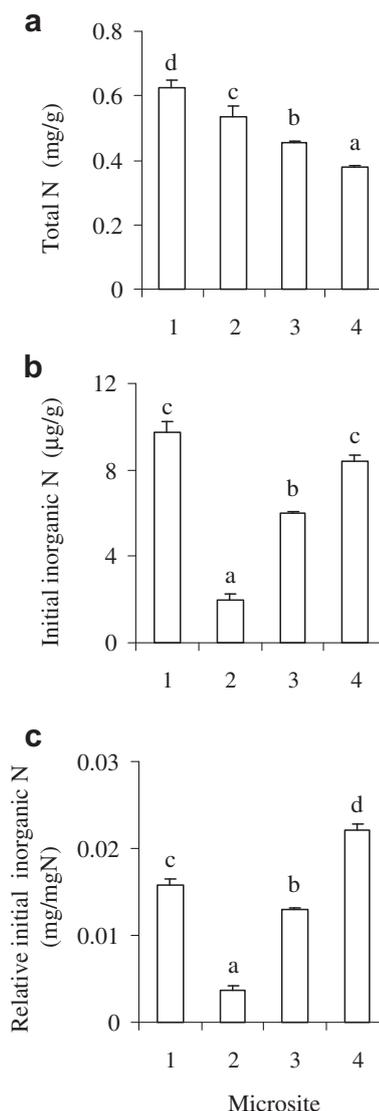


Fig. 2. Mean values of a. total N, b. initial inorganic N, and c. initial relative inorganic N (inorganic N per unit total soil N) in soil of plant patches and inter-patch areas of conserved (microsites 1 and 2, respectively) and disturbed by grazing (microsites 3 and 4, respectively) vegetation states. Vertical lines indicate one standard error. Different lowercase letters indicate significant differences among microsites ($p < 0.05$).

and Bertiller, 2008; Carrera et al., 2008), and in other arid ecosystems (Whitford, 2002). Accordingly, leaf litter from conserved vegetation states was less recalcitrant (i.e. lower concentration of secondary compounds) and its decomposition and mineralization rates had larger variation among soil microsites differing in the levels of inorganic-N than leaf litter from disturbed vegetation states. Non-recalcitrant leaf litter decomposed faster on the soil associated with conserved plant patches and on the soil of disturbed inter-patches than in the other soil microsites. Both microsites had the highest values of soil inorganic N. The highest values of total and inorganic-N in soils of conserved plant patches could be associated with biotic and physico-chemical factors imposed by patch canopies usually creating resource islands favoring local conditions for the activity of soil microorganisms and organic matter accretion (Prieto et al., 2011; Zaady et al., 1996). Contrarily, in soils of disturbed inter-patch microsites, high values of inorganic-N could be attributable to localized inputs of N by sheep urine and feces (Bardgett and Wardle, 2003; Steffens et al.,

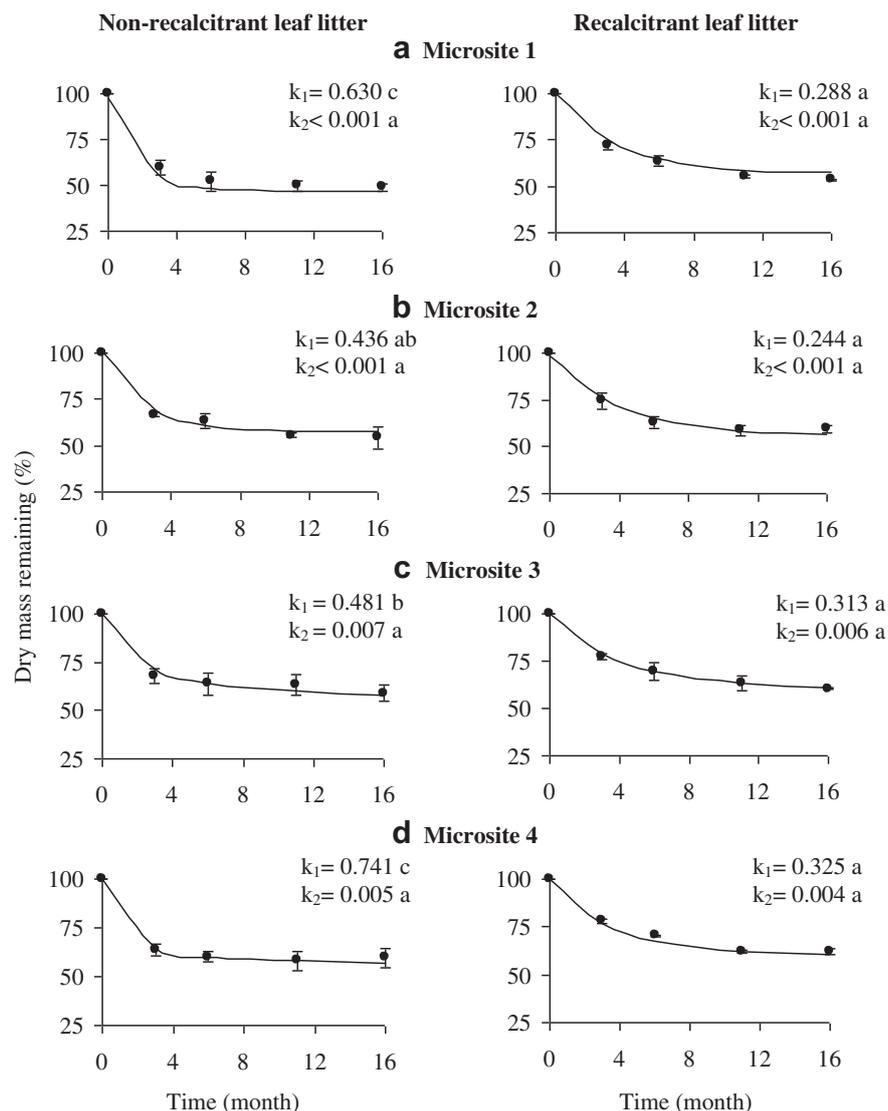


Fig. 3. Mean values \pm one standard error of remaining mass of non-recalcitrant and recalcitrant leaf litter as a function of time (black circles) and fitted double negative exponential curve (solid line) for microcosms with soil of plant patches and inter-patch areas of conserved (a. microsite 1 and b. microsite 2, respectively) and disturbed by grazing (c. microsite 3 and d. microsite 4, respectively) vegetation states. Different lowercase letters indicate significant differences in decomposition rate of metabolic fraction (k_1) and in recalcitrant fraction (k_2) of leaf litter among microsites ($p < 0.05$).

2008; Wardle, 2002). Under these conditions, the addition of a labile carbon source such as non-recalcitrant leaf litter could enhance the growth and activity of soil microorganisms and litter decomposition rates (Wardle et al., 2002) but also the saprophytic

activity increasing N immobilization (Ald, 2003), retaining N in labile forms (Mazzarino et al., 1998).

In contrast, recalcitrant leaf litter decomposed at similar rates on soil of all microsites suggesting a direct effect of secondary compounds on decomposer microorganisms. Structural carbon pools such as lignin and other cell wall components are resistant to enzymatic attack and microbial degradation (Hoorens et al., 2003). Moreover, phenolic compounds may affect decomposability by retaining N in litter through the formation of phenol–protein complexes and/or inactivation of microbial enzymes (Aerts and Chapin, 2000). Both, phenolics and lignin may interfere in decomposer metabolism, decelerating litter decay (Aerts and Chapin, 2000; Lambers et al., 2000). Accordingly, the reduction of total soil N under grazing disturbance could not be only attributable to the reduction in total and perennial grass cover (increasing inter-patch areas without plants) but also to the increase in litter recalcitrance, slowing down N-cycling at ecosystem level.

In summary, as predicted, leaf litter from conserved vegetation states was less recalcitrant and its rates of decomposition and N

Table 2

Mean values \pm one standard error of potential N mineralization in soil under non-recalcitrant and recalcitrant leaf litter of plant patches and inter-patch areas of conserved (C, microsites 1 and 2, respectively) and disturbed by grazing (D, microsites 3 and 4, respectively) vegetation states. Different lowercase letters indicate significant differences among microsites ($p < 0.001$).

Microsite	Potential N mineralization ($\mu\text{g/g}$)	
	Under leaf litter of C (non-recalcitrant leaf litter)	Under leaf litter of D (recalcitrant leaf litter)
1	135.7 \pm 1.8 e	97.5 \pm 3.1 d
2	62.3 \pm 3.6 b	61.0 \pm 3.4 b
3	80.3 \pm 1.5 c	75.4 \pm 3.0 c
4	62.4 \pm 4.9 b	44.2 \pm 1.5 a

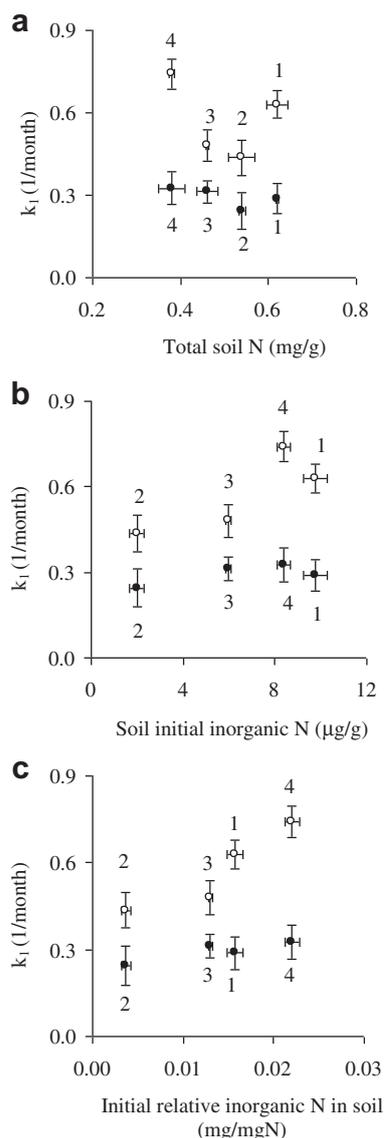


Fig. 4. Variation of decomposition rate of metabolic fraction (k_1) of non-recalcitrant (\circ) and recalcitrant (\bullet) leaf litter in relation to **a.** total soil N, **b.** initial inorganic N and **c.** initial relative inorganic N (inorganic N per unit total soil N) in soils of plant patches and inter-patch areas of conserved (1 and 2, respectively) and disturbed by grazing (3 and 4, respectively) vegetation states. Vertical and horizontal lines indicate one standard error.

Table 3
Stepwise regression between soil potential N mineralization in soils of conserved and disturbed by grazing vegetation states under non-recalcitrant and recalcitrant leaf litter as dependent variable and total soil N and dry mass remaining of leaf litter in litterbags as independent variables.

Model	n	r ²	F	Coefficient
Potential N mineralization in soil under non-recalcitrant leaf litter				
Total soil N	20	0.94	187.76	253.45***
Dry mass remaining of leaf litter		0.95		-0.76*
Constant				ns
Potential N mineralization in soil under recalcitrant leaf litter				
Total soil N	20	0.97	587.32	140.41***
Dry mass remaining of leaf litter				ns
Constant				ns

*** $p < 0.001$, * $p < 0.05$, ns: non-significant.

mineralization in the associated soil showed larger variation among soil microsites differing in the levels of inorganic-N than recalcitrant litter. Accordingly, microsites with non-recalcitrant litter could exhibit high decomposer activity and nutrient release offering important niches of regeneration for acquisitive perennial herbaceous plants such as perennial grasses with faster growth and higher N demands than shrubs (Luzuriaga and Escudero, 2008). In contrast, microsites with recalcitrant litter, independently of N levels in soil could decelerate N cycling thus preventing or reducing the establishment and growth of acquisitive plant species such as perennial grasses and alternatively promoting the establishment and dominance of conservative species such as evergreen shrubs in plant canopies (Luzuriaga and Escudero, 2008). These findings highlight the importance of the combined effects of soil properties and leaf litter quality on decomposition and N cycling processes affecting regeneration niches and the reestablishment of plants with different ecological strategies with eventual consequences for resistance and resilience and management strategies of grazed arid ecosystems (Gregory et al., 2009).

5. Conclusions

The changes in the canopy structure induced by grazing lead to an increase in leaf litter recalcitrance, reducing litter decay and rates of soil N mineralization, independently of soil N levels. These conditions could prevent or reduce the reestablishment and growth of perennial grasses and alternatively could promote the establishment and dominance of evergreen shrubs in plant canopies disturbed by grazing. The addition of non-recalcitrant litter on soils of disturbed inter-patch microsites with high values of inorganic-N could enhance decomposer activity and nutrient release offering important niches of regeneration for plant preferred by herbivores such as perennial grasses with faster growth and higher N demands than shrubs. This, in turn, is important in relation to plant managerial strategies focused on the reestablishment of plant cover and ecosystem services in areas severely disturbed by grazing.

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