



# Decomposition of and nutrient dynamics in leaf litter and roots of *Poa ligularis* and *Stipa gynerioides*

Alicia S. Moretto, Roberto A. Distel\*

Departamento de Agronomía, CERZOS/CONICET, Universidad Nacional del Sur, Avenida Colon 80,  
8000 Bahía Blanca, Argentina

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## Abstract

A field experiment was conducted in a temperate semi-arid grassland of central Argentina to determine mass loss and P and N concentrations of decaying leaf litter and roots of *Poa ligularis* (high-quality litter) and *Stipa gynerioides* (poor-quality litter). Leaf litter and roots of each species were incubated on sites dominated by *P. ligularis* and on sites dominated by *S. gynerioides*, to separate species from site effects. The experiment lasted up to 21 months. Mass loss of leaf litter and roots was higher ( $p < 0.01$ ) in *P. ligularis* than in *S. gynerioides*. Mass loss of leaf litters were higher ( $p < 0.01$ ) on *P. ligularis* sites, whereas mass loss of roots were similar ( $p > 0.05$ ) on both type of sites. Both species showed similar pattern of P and N dynamics in the leaf litter and roots, but net mineralization was higher ( $p < 0.01$ ) in *P. ligularis* than in *S. gynerioides*.

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## 1. Introduction

Decomposition is a fundamental process of ecosystem functioning because its close link to nutrient supply for plant growth (Lambers et al., 1998). The dynamic of decomposition is strongly influenced by the inherent quality of the litter, environmental conditions, and the available decomposer community (Swift et al., 1979). In general, high carbon:nitrogen (C:N) ratio and high lignin concentration

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\*Corresponding author. Tel.: +54-291-486-1124; fax: +54-291-486-1527.

E-mail address: [cedistel@criba.edu.ar](mailto:cedistel@criba.edu.ar) (R.A. Distel).

translate into slow decomposition and nutrient immobilization, whereas low C:N ratio and low lignin concentration result in fast decomposition and nutrient mineralization (Hobbie, 1992; Van Vuuren et al., 1993; Berendse, 1994; Grime et al., 1996). Species with these characteristics are commonly referred as poor-quality litter species and high-quality litter species, respectively (Hobbie, 1992). Plants can also differentially influence microclimate, soil properties, soil organisms (Callaway, 1995) and, consequently, the rates of decomposition and nutrient dynamics.

*Poa ligularis* and *Stipa gynerioides* are perennial C<sub>3</sub> grasses native to temperate semi-arid grasslands of central Argentina. The former species produces high-quality live biomass and litter, whereas the later species produces poor-quality live biomass and litter (Distel et al., 2000; Rabotnikof et al., 2000). Domestic livestock (cattle, sheep, goat) shows high selectivity for *P. ligularis* and rejection for *S. gynerioides* (Pisani et al., 2000), which is associated with a decrease in the abundance of the former and an increase in the abundance of the later species in grazed areas (Llorens, 1995; Distel and Bóo, 1996, pp. 117–118). Therefore, if decomposition and nutrient mineralization are lower in *S. gynerioides* than in *P. ligularis*, this shift in species composition may slow down the rate of ecosystem nutrient cycling. It need to be considered, however, that the rate of nutrient cycling is determined by both the nutrient release rate and the total amount of litter (above- and below-ground) that is produced per unit ground area (Chapin, 1991, pp. 68–88). The purpose of the present study was to compare mass loss and P and N concentrations in decaying leaf litter and roots of *P. ligularis* with that of *S. gynerioides*. Species effects were separated from site effects by incubating leaf litter and roots of both species on sites dominated by *P. ligularis* and on sites dominated by *S. gynerioides*. Ongoing research is evaluating litter production in both species.

## 2. Materials and methods

### 2.1. Study site

The research was conducted in the Caldén District (Cabrera, 1976), on an upland site located in the south-eastern zone of La Pampa province in central Argentina (38°45'S; 63°45'W) (Fig. 1). The site has not been grazed by domestic animals for ~20 years. The climate is temperate, semi-arid (a climate diagram of the region is provided by Distel and Fernández, 1987). Mean monthly air temperatures range from a low of 7°C in July to a high of 24°C in January, with an annual mean of 15°C. Mean annual rainfall is 344 mm, with peaks in October and March. The more severe droughts occur during summer. Precipitation at the study site during the experimental period was 375 and 560 mm, in 1998 and 1999, respectively. Dominant soils are coarse textured Calciustolls. A petrocalcic horizon is commonly found at depths of 60–80 cm. The physiognomy of the vegetation is grassland with isolated woody plants. The most abundant species in the herbaceous layer are perennial C<sub>3</sub> cool-season bunchgrasses (Distel and Peláez, 1985). *P. ligularis* is the dominant species, but patches dominated by *S. gynerioides* are common.

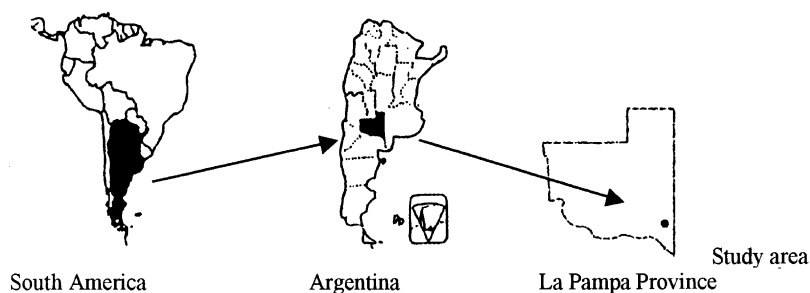


Fig. 1. Location of the study area.

## 2.2. Experimental design

In November of 1997, plants of *P. ligularis* and *S. gynerioides* were collected at their natural growing sites and taken to the laboratory. The above-ground portion of each plant was sampled for leaf material that had recently senesced and that was still connected to the plant. The below-ground portion was sampled for roots after removing the soil by gently washing with tap water. Leaf litter and roots were air dried to constant weight at room temperature, cut into 10-cm long pieces, and enclosed in  $10 \times 15 \text{ cm}^2$  bags (5 g per bag) from polyethylene gauze (0.35 mm mesh). Prevalent functional groups of soil organisms in the region are Acari, Collembola, and Nematoda (Perez et al., 1987). For each grass species, subsamples of the leaf litter and roots were weighed air-dry and again after 48 h in an oven at  $60^\circ\text{C}$ , in order to calculate initial oven-dry weights of the incubated material. In March, 1998, the leaf litter and root bags were transferred to sites with a continuous cover either of *P. ligularis* or *S. gynerioides*. Four bags containing *P. ligularis* litter and four bags containing *S. gynerioides* litter were placed on each of 10 plots at each type of site. The bags were placed horizontally on the soil surface and secured in place with nails. The same procedure was followed for roots, except that root bags were laid horizontally at the bottom of a hole (5 cm deep) and covered with the removed soil. Ten replicate leaf litter bags and 10 replicate root bags were collected for each species at each type of site after 4, 9, 16, and 21 months of incubation. In the laboratory, the leaf litter and roots were removed from the bags, cleaned to remove any extraneous material, and weighed after drying at  $60^\circ\text{C}$  for 48 h. Corrections for inorganic contaminants were made after determining loss on ignition of all samples (4 h,  $600^\circ\text{C}$ ). Potential errors can be associated with ignition temperature. Temperatures below  $500^\circ\text{C}$  may result in incomplete oxidation of organic matter (Gallardo et al., 1987), whereas temperatures higher than  $500^\circ\text{C}$  may volatilize inorganic carbonates (Schulte and Hopkins, 1996), particularly in coarse textured Calciustolls. The last potential problem may have influenced absolute values of mass loss on ignition at  $600^\circ\text{C}$  in the present study. However, leaf litter and roots from both species were subjected to the same ignition temperature, which validates between treatment comparisons.

Initial leaf litter and root samples were analysed for C, N, P, and lignin, whereas subsequent samples were analysed for N and P. Carbon was determined by dry combustion with an elemental analyser (Leco, model CR-1). Nitrogen was determined by semi-micro Kjeldahl, P according the colorimetric technique of [Olsen and Dean \(1965, pp. 1035–1049\)](#), and lignin using the detergent method ([Goering and Van Soest, 1970](#)).

Soil temperature and soil moisture were periodically measured during the experimental period at both type of sites. Soil temperature (0–3 cm depth) was measured with copper–constantan thermocouples ( $n = 6$ ) at 1400 h, whereas soil moisture (0–15 cm depth) was determined gravimetrically ( $n = 5$ ).

Mass and N and P concentration data were expressed as percentage of initial values on an ash-free basis. The expression of the N and P contents of the leaf litter and root bags as a percentage of the initial content allowed for the determination of net N and P dynamics. Data were analysed by a two-way (species-site, and time) analysis of variance (ANOVA). Leaf litter and root data were analysed separately. Because for mass of roots the variance was heterogeneous, the data were arcsine-square root transformed prior to analysis. Tukey-Kramer tests were performed to test differences between species-site treatments when  $F$  values from ANOVAs were significant ( $p < 0.05$ ). An exponential decay model ([Olson, 1963](#)) was used to calculate de decay constants ( $k$  values) for the first and second year of incubation. Pearson’s linear correlation coefficients were calculated for the percentage mass loss after 21 months of incubation and initial leaf litter and root quality parameters.

3. Results

Initial leaf litter and roots of *P. ligularis* were higher ( $p < 0.05$ ) in N and P, and lower ( $p < 0.05$ ) in lignin, C/N ratio, lignin/N ratio and lignin/P ratio than was *S. gynerioides* ([Table 1](#)). In general, the differences between species in leaf litter chemistry were higher than their differences in root chemistry.

Mass loss of leaf litter and roots varied significantly ( $p < 0.001$ ) with time and species-site treatments ([Fig. 2, Table 2](#)). There was no species-site by time interaction

Table 1  
Initial chemical composition of leaf litter and roots in *P. ligularis* and *S. gynerioides*. Values are means  $\pm$  1 S.E. ( $n = 5$ ). Means within a column and plant part followed by different letters are significantly different ( $p < 0.05$ )

	Lignin (%)	N (%)	P (%)	C/N	Lignin/N	Lignin/P
Leaf litter						
<i>P. ligularis</i>	4.4 $\pm$ 0.4a	1.4 $\pm$ 0.03a	0.06 $\pm$ 0.002a	29 $\pm$ 0.5a	3 $\pm$ 0.3a	72 $\pm$ 7.8a
<i>S. gynerioides</i>	6.4 $\pm$ 0.2b	0.7 $\pm$ 0.01b	0.03 $\pm$ 0.003b	56 $\pm$ 1.2b	9 $\pm$ 0.3b	194 $\pm$ 13b
Roots						
<i>P. ligularis</i>	14.0 $\pm$ 0.5a	0.9 $\pm$ 0.02a	0.06 $\pm$ 0.002a	42 $\pm$ 0.6a	15 $\pm$ 0.8a	241 $\pm$ 13a
<i>S. gynerioides</i>	20.0 $\pm$ 0.5b	0.7 $\pm$ 0.02b	0.04 $\pm$ 0.001b	64 $\pm$ 1.5b	31 $\pm$ 0.8b	544 $\pm$ 18b

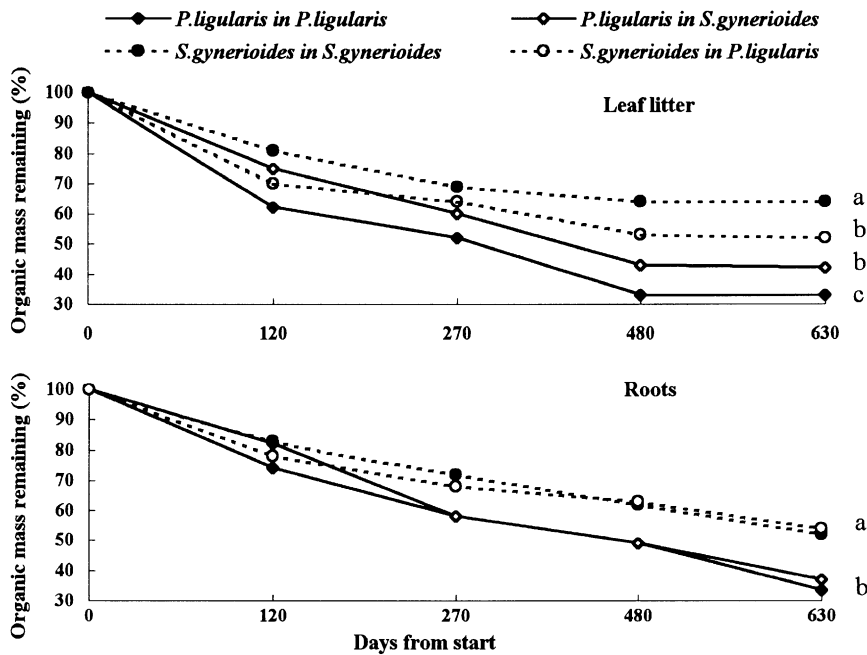


Fig. 2. Mass remaining (as percentage of initial amount) through time for leaf litter and roots of *P. ligularis* and *S. gynerioides* incubated on both sites. Different letters at the end of the incubation period indicate significant average differences ( $p < 0.01$ ) among site-species treatments. The SEM are 0.65% for leaf litter and 0.71% for roots.

Table 2  
Analysis of variance of species-site and time for leaf litter and roots

Source of variation	Leaf litter			Roots		
	Mean square	DF	F value	Mean square	DF	F value
Time	7252.8	3	117.4***	9966.1	3	135.7***
Species-site	2132.0	3	34.52***	2421.1	3	32.1***
Interaction	104.1	9	1.68 ns	80.5	9	1.1 ns
Error	61.7	144		73.4	144	

Asterisks indicate  $p < 0.001$ .

( $p > 0.05$ ). On average, mass loss of leaf litter and roots was higher ( $p < 0.01$ ) in *P. ligularis* than in *S. gynerioides*. The site of incubation influenced mass loss of leaf litter only. Mass loss of *P. ligularis* was lower ( $p < 0.01$ ) at *S. gynerioides* sites, whereas mass loss of *S. gynerioides* was higher ( $p < 0.01$ ) at *P. ligularis* sites.

All exponential regressions used to describe mass loss through time were significant (average  $r^2 = 0.92$  and  $0.96$  for leaf litter and roots, respectively). The  $k$  values, which reflect the first and second year of decay, emphasize the faster decay of leaf litter and roots in *P. ligularis* than in *S. gynerioides* (Table 3). Percentage mass loss of

Table 3

First- and second-year decomposition constants ( $k$  values) for leaf litter and roots of *P. ligularis* and *S. gynerioides* incubated on both sites. Values are means  $\pm$  1 S.E. Means within a column and plant part followed by different letters are significantly different ( $p < 0.05$ )

Species-site treatments	$k$ values	
Leaf litter	First year	Second year
<i>P. ligularis</i> in <i>P. ligularis</i>	$0.42 \pm 0.02a$	$0.30 \pm 0.03a$
<i>P. ligularis</i> in <i>S. gynerioides</i>	$0.48 \pm 0.04a$	$0.31 \pm 0.03a$
<i>S. gynerioides</i> in <i>S. gynerioides</i>	$0.21 \pm 0.01b$	$0.11 \pm 0.005b$
<i>S. gynerioides</i> in <i>P. ligularis</i>	$0.26 \pm 0.01b$	$0.10 \pm 0.009b$
Roots		
<i>P. ligularis</i> in <i>P. ligularis</i>	$0.30 \pm 0.03a$	$0.23 \pm 0.02a$
<i>P. ligularis</i> in <i>S. gynerioides</i>	$0.31 \pm 0.02a$	$0.22 \pm 0.02a$
<i>S. gynerioides</i> in <i>S. gynerioides</i>	$0.20 \pm 0.009b$	$0.17 \pm 0.01b$
<i>S. gynerioides</i> in <i>P. ligularis</i>	$0.20 \pm 0.02b$	$0.14 \pm 0.01b$

Table 4

Pearson linear correlation coefficients ( $r$ ) ( $n = 10$ ) between mass loss after 630 days and initial litter quality parameters

	Leaf litter	Roots
Lignin	$-0.77^{**}$	$-0.74^*$
N	$0.89^{***}$	$0.76^*$
P	$0.89^{***}$	$0.76^*$
C:N	$-0.90^{***}$	$-0.9^{***}$
Lignin:N	$-0.90^{***}$	$-0.90^{***}$
Lignin:P	$-0.87^{**}$	$-0.87^{**}$

Asterisks indicate significant correlation between the two variables at 0.05 (\*), 0.01 (\*\*) and 0.001 (\*\*\*) probability levels.

leaf litter and roots after 21 months of incubation was positively related with initial N and P concentrations, and negatively related with initial lignin concentration, C/N ratio, lignin/N ratio and lignin/P ratio (Table 4).

The P and N contents of the leaf litter and root bags varied significantly ( $p < 0.001$ ) with time and species-site treatments (Fig. 3). The interaction time by species-site was significant ( $p < 0.01$ ) for P and N contents of the leaf litter only. On average, there was no site effect ( $p > 0.05$ ) on the dynamic of P and N in the leaf litter and root of both species, and net mineralization of N and P was greater ( $p < 0.01$ ) in *P. ligularis* than in *S. gynerioides*. In both species, there was net P and N mineralization from the leaf litter in the first 4 months of incubation, whereas there was a tendency to immobilize P and N in the last 17 months of incubation. Immobilization was much more marked for P than for N. Moreover, at the end of the incubation period there was net immobilization of P in the leaf litter of *S. gynerioides*. On the other hand, there was initially (first 16 months of incubation) a slow net mineralization of

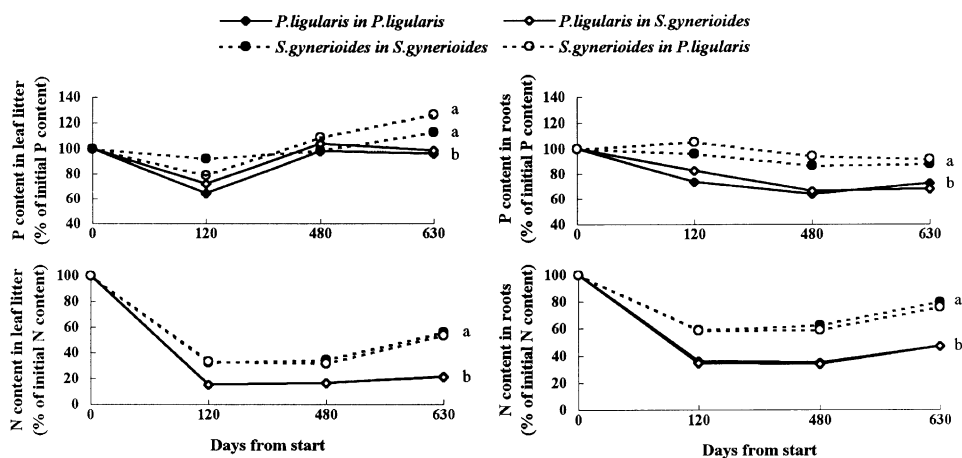


Fig. 3. Nitrogen and phosphorus content (as percentage of initial content) in leaf litter and roots of *P. ligularis* and *S. gynerioides* incubated on both sites. Different letters at the end of the incubation period indicate significant average differences ( $p < 0.01$ ) among site-species treatments. The SEM are 0.41% for P-leaf litter, 0.46% for P-roots, 0.31% for N-leaf litter, and 0.61% for N-Roots.

P from the roots of both species, followed by immobilization of P toward the end of the incubation period. Also, there was a net mineralization of N from the roots of both species in the first four months of incubation, and then a tendency to immobilize N.

#### 4. Discussion

In both species leaf litter and roots showed similar decay rate (Fig. 2). Although root quality was lower than leaf litter quality, roots were buried and probably experienced better environmental conditions (moisture, nutrients) for decomposition. Decomposition rates of leaf litter and roots were higher than decomposition rates measured for *P. ligularis* and *S. tenuissima* (low-quality litter grass) in a previous study at the same site (Moretto and Distel, 2001). The beginning of the incubation in the present study was particularly wet (Fig. 4), which may explain the observed differences. Rates of surface litter loss have shown to be strongly correlated with actual rainfall in arid environments (Strojan et al., 1987). First-year decomposition constants for leaf litter of the studied species (Table 3) were in the range reported for forbs and graminoids in temperate zones (0.18–0.40) (Aerts and Chapin III, 2000). Mass loss of leaf litter through time in *P. ligularis* was comparable to values reported for *Festuca ovina* ( $C_3$  grass) (Koukoura, 1998) and mixed-grass prairie dominated by *S. comata* and *Koeleria gracilis* (Köchy and Wilson, 1997). On the other hand, leaf litter decomposition in *S. gynerioides* was much similar to leaf litter decomposition of  $C_4$  grasses like *Schizachyrium scoparium* (Pastor et al., 1987).

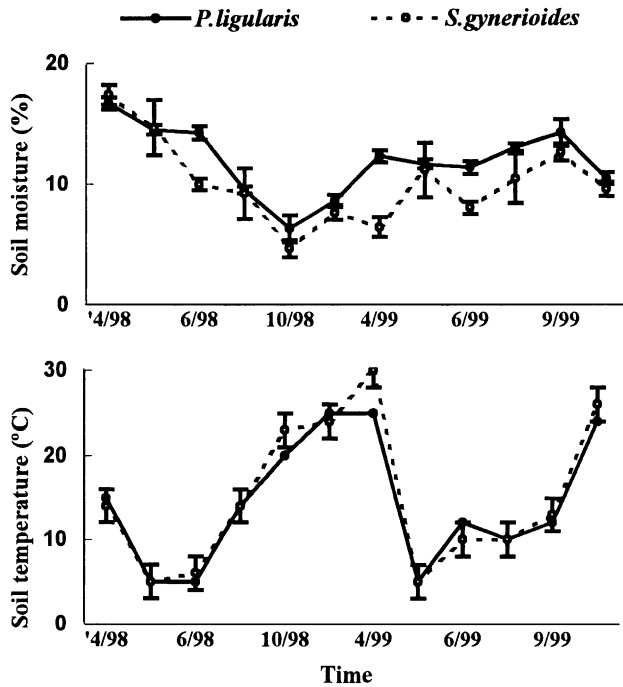


Fig. 4. Soil temperature (0–3 cm depth) and moisture (0–15 cm depth) on *P. ligularis* and *S. gynerioides* sites. Values are means of 10 samples  $\pm 1$  S.E.

and *Andropogon gerardii* (Seastedt, 1988). However, it is important to note the particularly high net mineralization of N in the studied species (Fig. 3) when compared with the C<sub>3</sub> and C<sub>4</sub> grasses previously mentioned, whose implications are discussed below.

Our results indicate that decomposition of leaf litter was determined by both chemical composition of the material and characteristics of the site, whereas decomposition of roots was determined by their chemical composition only (Fig. 2). Although there was no much difference between sites in soil temperature and soil moisture (Fig. 4), the differences in the accumulation of above-ground death biomass between species (larger in *S. gynerioides* than in *P. ligularis*) may somehow change the microenvironment under which leaf litter decomposed. For example, temperature in the litter bags may have been higher in *P. ligularis* sites because they were more exposed to solar radiation. Similarly, they were probably more exposed to the direct effects of rainfall. Microsite differences, including structural factors that influence microclimate, have been shown to affect mass loss of leaf litter in arid conditions (Cepeda-Pizarro and Whitford, 1990). On the other hand, the chemical composition of the material appears to be a critical factor in determining the decomposition rate. The faster decomposition of the leaf litter and roots of *P. ligularis* was associated with initially higher N and P concentration, lower lignin



concentration, and lower C:N, lignin:N, and lignin:P ratios both in leaf litter and roots (Tables 1–4). All or some of these chemistry parameters were shown to be strongly correlated with leaf litter decay rates in many studies conducted in mesic ecosystems (e.g., Wedderburn and Carter, 1999; Hartmann, 1999; Perez-Harguindeguy et al., 2000; Aerts and Chapin III, 2000), and with decomposition rates of roots in desert soils (Mun and Whitford, 1998). Contrarily, in desert environments physical weathering appears to be the most important determinant of litter mass losses (Montaña et al., 1988; Moorhead and Reynolds, 1989). For example, Schaefer et al. (1985) did not find correlation between rates of mass losses of six litter types and initial percent of lignin, C:N ratio or lignin:N ratio in a North American desert.

In general, the higher net mineralization of P and N from the leaf litter and roots of *P. ligularis* (Fig. 3) were consistent with the faster decomposition rate of this species. Otherwise, the pattern of the dynamic of P and N was similar in both species. At the beginning of the incubation period net mineralization of P and N was probably related to leaching of the more labile compounds. Then, the prevalence of immobilization of N and P in the leaf litter and roots may have been due to microbial immobilization. Uptake of P and N from the soil solution may be needed for decomposition to progress (Swift et al., 1979). However, immobilization of P and N in the leaf litter of both species toward the end of the incubation period occurred when decomposition rate was relatively low, which suggest that accumulation of P and N was not only caused by microbial immobilization. Mechanisms such as translocation of P from fungal hyphae (Aerts and Chapin III, 2000) and N contamination with organic matter (Van Vuuren et al., 1993) may have occurred.

Overall, there was a large difference between the dynamic of P and the dynamic of N in the leaf litter and roots of both species. Initial net mineralization of N was much larger than initial net mineralization of P, which suggest that P is more important than N as control of initial leaf litter and root decay in both species. The N:P ratio varied between 23–25 and 16–17 for leaf litter and roots, respectively (Table 1). This implies that these substrates may have a relative shortage of P for decomposers, because the N:P ratio in bacterial and fungal cells is in the range of 10–15 (Swift et al., 1979). In concordance, on the average net mineralization of P from roots (lower N:P ratio) was higher than net mineralization of P from leaf litter (higher N:P ratio).

Our results suggest that the replacement of high-quality litter grasses by low-quality litter grasses in grasslands may imply a reduction in the rate of ecosystem nutrient cycling. Low-quality grasses have relatively low tissue nutrient concentrations, and relatively low decomposition and mineralization rates. Moreover, low-quality species generally have low potential productivity and low tissue turnover rate (Aerts and Chapin III, 2000), which further reduce the rate of nutrient cycling. In the study site total soil mineral N availability was consistently higher in patches dominated by *P. ligularis* than in patches dominated by *S. tenuissima* (low-quality litter grass) (Moretto and Distel, 2000). The probable limitation in nutrient supply imposed by low-quality litter grasses may represent a positive feedback, because

these species are adapted to shortage of nutrients (Aerts and Chapin III, 2000). This kind of positive feedback has recently been highlighted by several authors (Berendse, 1994; Jones et al., 1994; Aerts, 1995; Wedin, 1995, pp. 253–262). However, compared with low-quality litter grasses from humid grasslands (Wedin, 1995, 1999), our results suggest a relatively low potential to immobilize nutrients in the low-quality litter grasses from semi-arid grasslands. The relatively low potential to immobilize nutrients in roots is particularly relevant because the ratio below-ground to above-ground biomass can be as high as 7:1 in semi-arid grasslands (Distel and Fernández, 1986).

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