

Decomposition and nutrient dynamic of leaf litter and roots from palatable and unpalatable grasses in a semi-arid grassland

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Abstract

A field experiment was conducted in a temperate semi-arid grassland of central Argentina to test the hypothesis that decomposition of and nutrient release from leaf litter and roots are faster in *Poa ligularis* and *Stipa clarazii* (high-nutrient, palatable grasses) than in *S. tenuissima* (low-nutrient, unpalatable grass). Leaf litter and roots of each species were incubated in 0.35 mm mesh bags for 21 months at their source sites. Leaf litter decomposition was faster ($P < 0.01$) in the palatable than in the unpalatable species and, on average, root decomposition was faster ($P < 0.01$) in *S. clarazii* than in *P. ligularis* and *S. tenuissima*. At the end of the incubation period nitrogen (N) and phosphorus (P) release from the leaf litter was higher ($P < 0.01$) in the palatable than in the unpalatable species, whereas there was no difference ($P > 0.05$) among species in N and P release from the roots. The results on leaf litter support the hypothesis that decomposition and nutrient release are faster in the palatable than in the unpalatable grasses, whereas the results on roots did not support this hypothesis. Moreover, since below-ground production represents the major input of new soil organic matter in the system, the N and P dynamics of roots suggest a low capacity to immobilize nutrients in both palatable and unpalatable grasses. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Leaf litter decomposition; Nutrient dynamics; Palatable/unpalatable grasses; Semi-arid grasslands; Root decomposition

1. Introduction

Decomposition is a fundamental process of ecosystem functioning because it is a major determinant of nutrient cycling. The rate of plant decomposition and nutrient release varies with a number of factors, including the nature of the plant material (Swift et al., 1979). In general, low-nutrient species produce litter that is more difficult to decompose than litter from high-nutrient species (Hobbie, 1992; Van Vuuren et al., 1993; Berendse, 1994; but see Berg et al., 1996; Aerts and De Caluwe, 1997). Furthermore, Grime

et al. (1996) found a significant positive correlation between leaf palatability and litter decomposition rate in an study involving 54 vascular plant species.

The role of plant tissue chemistry and its decomposition on nutrient cycling in grasslands has been recently reviewed and conceptualized by Wedin (1995, 1999). In native humid grasslands late-seral dominant grasses tend to have low tissue nitrogen (N) concentrations and high carbon:nitrogen (C:N) ratios and lignin concentrations, which translate into slow decomposition and nutrient immobilization. In contrast, in arid and semiarid grasslands late-seral dominant grasses tend to have high tissue N concentrations and low C:N ratios and lignin concentrations, which result in fast decomposition and nutrient mineralization. Overgrazing by domestic livestock is

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frequently associated with changes in species composition in native grasslands (e.g. Westoby et al., 1989; Milchunas and Lauenroth, 1993; Milton et al., 1994). In semi-arid grasslands of central Argentina, high-nutrient grasses frequently give way to invasion by low-nutrient grasses under conditions of long-term heavy grazing (Llorens, 1995; Distel and Bóo, 1996). In this system, high-nutrient grasses are palatable to ungulate grazers, whereas low-nutrient grasses are unpalatable to ungulate grazers (i.e. they are consumed either to a greater or to a lower degree than expected based on their abundance, respectively) (Distel et al., 2000; Pisani et al., 2000). Our study addresses the question of whether the palatable and unpalatable grasses native to the temperate semi-arid grasslands of central Argentina differ in decomposition rate and nutrient release from leaf litter and roots.

The objective of this study was to compare decomposition and N and P dynamics of *Poa ligularis* and *Stipa clarazii* (palatable grasses) leaf litter and roots, incubated at their source sites, with that of *S. tenuissima* (unpalatable grass) incubated at its source site. We hypothesized that leaf litter and roots from the palatable grasses decompose and release nutrients faster than leaf litter and roots from the unpalatable grasses.

2. Materials and methods

2.1. Study area

The research was conducted in the Caldén District (Cabrera, 1976), on an upland area located in the south-eastern zone of La Pampa province in central Argentina (38°45'S; 63°45'W). The 20 ha area has not been grazed by domestic animals for ~20 years. The climate is temperate, semi-arid. Mean monthly average day time 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 400 mm, with peaks in October and March. The more severe droughts occur during summer. Precipitation during the experimental period was 530 and 548 mm, in 1996 and 1997, respectively. Dominant soils are coarse textured Calcicustolls. 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 C₃ cool-season bunchgrasses (Distel and Peláez, 1985). The palatable grasses (*S. clarazii*, *P. ligularis*, *S. tenuis*, *Piptochaetium napostaense*) are the dominant species, but individuals and patches of unpalatable grasses (*S. gynerioides*, *S. tenuissima*, *S. trichotoma*, *S. speciosa*, *S. brachichaeta*) are common. The leaves of the palatable grasses are higher in N concentration and lower in C:N ratio and lignin concentration than those of the unpalatable grasses (Moretto and Distel, 1997). These differences in chemical composition translate into a high acceptability of palatable grasses and a low acceptability of unpalatable grasses by ungulate grazers (Bóo et al., 1993).

2.2. Experimental design

In November 1995, plants of the two palatable species (*P. ligularis*, *S. clarazii*) and of the unpalatable species (*S. tenuissima*) were collected at their natural growing sites and taken to the laboratory. The aboveground 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 that were still attached to the crown after removing the soil by gently washing with tap water. It is probable that root samples contained both living and recently dead roots. Leaf litter and roots were air dried to constant weight at room temperature, cut into 10 cm long pieces, and enclosed in 10 cm × 15 cm bags (5 g per bag) from polyethylene gauze (0.35 mm mesh). A survey of soil fauna in the region revealed that soil fauna larger than 0.35 mm is almost absent (Perez et al., 1987). For each studied species, a subsample of the leaf litter and roots were weighed air-dry and again after 48 h in an oven at 60°C, in order to calculate initial oven-dry weights of the material. On 15 March 1996, the leaf litter and root bags were transferred to native growing sites of each of the species. Within sites with a continuous cover either of *P. ligularis*, *S. clarazii* or *S. tenuissima*, 30 leaf litter bags were placed horizontally on the soil surface and 30 root bags were laid horizontally at the bottom of a hole (5 cm deep) and covered with the removed soil. At each sampling date, 10 leaf litter or root bag of each species were retrieved. In this way, 10 replicate leaf litter bags and 10 replicate root bags were collected for each species after 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 organic material, and weighed after drying at 60°C for 48 h. Corrections for inorganic contaminants (soil particles mainly) were made after determining loss-on-ignition of all samples (4 h, 600°C).

Initial leaf litter and root samples were analyzed for C, N, P, and lignin, whereas subsequent samples were analyzed for N and P. Carbon was determined by dry combustion with an elemental analyzer (Leco). Nitrogen was determined by semi-micro Kjeldahl, P according to the colorimetric technique of Olsen and Dean (1965), and lignin using the detergent method (Goering and Van Soest, 1970).

Soil temperature and soil moisture were periodically measured during the experimental period at the native growing sites of each species. Soil temperature (0–3 cm depth) was measured with copper–constantan thermocouples ($n = 6$) at 14.00 h, whereas soil moisture (0–15 cm depth) was determined gravimetrically ($n = 5$). Precipitation during the study period was measured with an automatic rain gauge located in the study area.

Mass loss and N and P release 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. All data were analyzed by a two-way (species and time) analysis of variance (ANOVA). Leaf litter and root data were analyzed separately. Mass loss of roots was arcsine-square root transformed prior to analysis to improve normality. Tukey–Kramer tests

were performed to test differences among species when F -values from ANOVAs were significant ($P < 0.05$). Pearson's 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 the palatable grasses (*S. clarazii* and *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 the unpalatable grass (*S. tenuissima*). The only exception was the similarity in N content of roots between *P. ligularis* and *S. tenuissima* (Table 1). Both groups of species differed more in leaf litter chemistry than in root chemistry.

The percentage mass remaining of leaf litter varied significantly ($P < 0.01$) with time and species (Fig. 1). The interaction time by species was not significant ($P > 0.05$). The leaf litter of the palatable grasses decomposed faster ($P < 0.05$) than that of the unpalatable grass. After 21 months of incubation the percentage mass remaining of leaf litter was 58, 59 and 78%, for *S. clarazii*, *P. ligularis*, and *S. tenuissima*, respectively. On the other hand, the percentage mass remaining of roots also varied significantly ($P < 0.01$) with time and species (Fig. 1), but there was a time by species interaction ($P < 0.05$). On average, the roots of *S. clarazii* decomposed faster ($P < 0.05$) than those of *P. ligularis* and *S. tenuissima*. After 21 months of incubation, the percentage mass remaining

Table 1
Initial chemical composition of ash-free leaf litter and roots^a

	Lignin (%)	N (%)	P (%)	C:N	Lignin:N	Lignin:P
Leaf litter						
<i>P. ligularis</i>	3.9 a	1.6 a	0.06 a	26 a	2.4 a	63 a
<i>S. clarazii</i>	4.9 b	1.8 b	0.06 a	23 a	2.7 a	82 b
<i>S. tenuissima</i>	7.9 c	0.9 c	0.02 b	49 b	8.7 b	370 c
Roots						
<i>P. ligularis</i>	13 a	1.1 a	0.06 a	35 a	11 a	227 a
<i>S. clarazii</i>	16 b	1.4 b	0.07 b	27 b	12 b	237 a
<i>S. tenuissima</i>	19 c	1.1 a	0.04 c	38 c	17 c	447 b

^a Values are means of five samples. Values within a column and plant part followed by different letters are significantly different ($P < 0.05$).

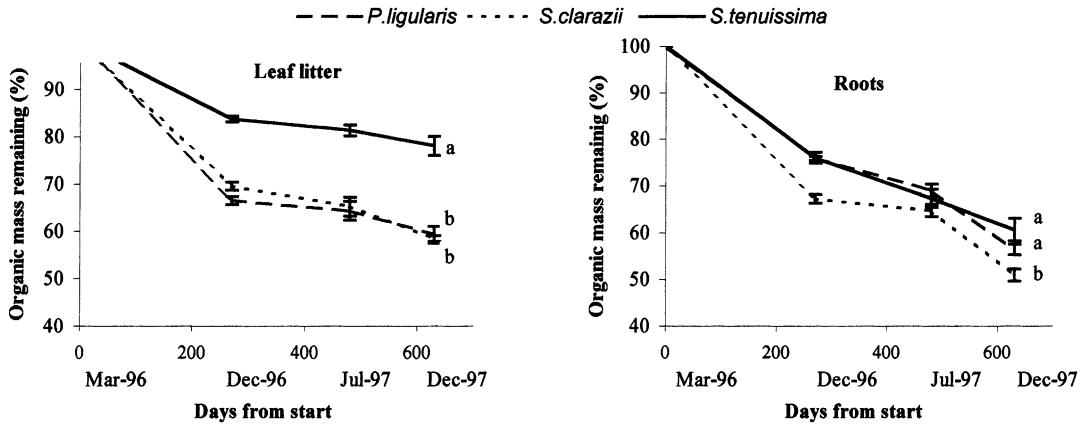


Fig. 1. Ash-free mass remaining through time of leaf litter and roots from *P. ligularis*, *S. clarazii* and *S. tenuissima*. Values are means of 10 samples \pm 1 S.E. At the end of the experiment values followed by different letters are significantly different ($P < 0.05$).

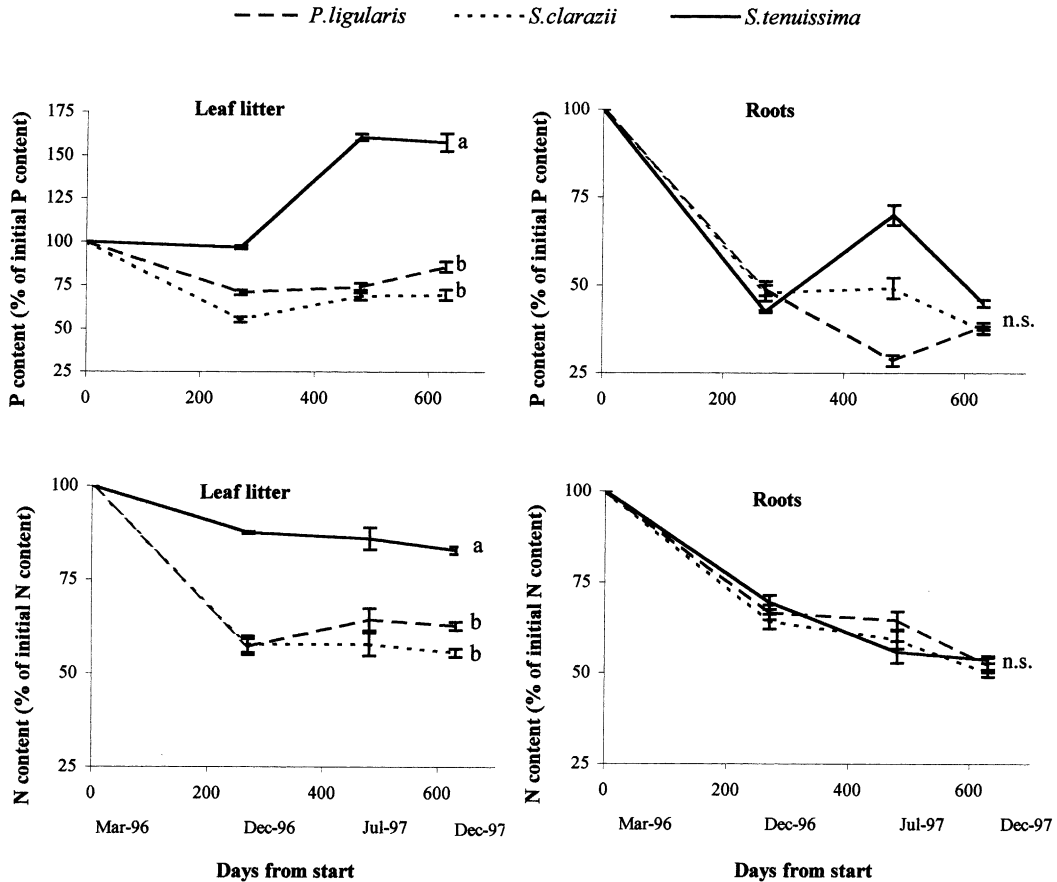


Fig. 2. Nitrogen and phosphorus content (as percentage of initial content) of ash-free leaf litter and roots from *P. ligularis*, *S. clarazii* and *S. tenuissima*. Values are means of five samples \pm 1 S.E. At the end of the experiment values followed by different letters are significantly different ($P < 0.05$); n.s. indicates differences not significant ($P > 0.05$).

of roots was 51, 56 and 61%, for *S. clarazii*, *P. ligularis*, and *S. tenuissima*, respectively.

The P and N content of the leaf litter and root bags (Fig. 2) varied significantly ($P < 0.01$) with time and species, except for the differences among species in N content of the root bags. The interaction time by species was significant ($P < 0.01$), except for the dynamic of N in the roots. In the first 9 months of incubation there was net P and N release from the leaf litter of the three species, except for P in *S. tenuissima*, whereas in the last 12 months of incubation there was a tendency to immobilize P and N in the leaf litter of all species. However, at the end of the incubation period there was net immobilization of P in the leaf litter of the unpalatable species but net release of P from the leaf litter of the palatable species. In the case of N, although there was net release from the leaf litter of all three species, it was lower ($P < 0.05$) in the unpalatable than in the palatable species. On the other hand, there were only minor differences among species in root P and N dynamics. There was a marked release of P and N in the first 9 months of incubation, and a slow tendency to release or immobilize P and N after that. At the end of the incubation period the percentage of P and N released from the roots of the unpalatable and palatable species was similar ($P > 0.05$).

4. Discussion

Our results only partly support the hypothesis that decomposition and nutrient release are faster in *P. ligularis* and *S. clarazii* (palatable species) than in *S. tenuissima* (unpalatable species). Although leaf litter decomposition (Fig. 1) and nutrient release (Fig. 2) were higher for the palatable grasses than for the unpalatable grass, there were no consistent differences between them in root decomposition and nutrient release. The exception were the roots of *S. clarazii*, which on average decomposed faster than the roots of *P. ligularis* and *S. tenuissima*. The overall similarities between the palatable and the unpalatable species in the decomposition and nutrient dynamics of roots is relevant because the ratio of below-ground to above-ground biomass can be as high as 7:1 in the study site (Distel and Fernández, 1986), indicating that root production and turnover represent the major input of new

soil organic matter in the system. It is necessary to notice that although part of the roots used in this study were probably live when collected, and might have not adequately represented the chemical composition of natural senesced roots, some evidence suggests minimal nutrient retranslocation from roots upon senescence (Oestertag and Hobbie, 1999; Wedin, 1999).

The greater differences between palatable and unpalatable grasses in leaf litter than in root decomposition and nutrient release were associated with a much higher initial difference between them in leaf litter chemistry than in root chemistry (Table 1). All the correlations between the percentage mass loss after 21 months of incubation and initial chemical parameters were much stronger for leaf litter than for roots (Table 2). Since our decomposition experiment was performed at the native growing sites of each species, it is not possible to separate the influence of litter chemistry from possible site differences in biotic and/or abiotic conditions. However, the similarities among sites in soil temperature and soil moisture (Fig. 3) and their proximity, suggest that conditions for decomposition were similar among them.

The P and N dynamics during the incubation period (Fig. 2) indicate a relatively low potential to immobilize nutrients in the leaf litter and roots of both palatable and unpalatable grasses. The exception was the marked tendency to immobilize P in the leaf litter of *S. tenuissima*, which was associated with the lowest initial P concentration (Table 1). When P concentration is low, considerable immobilization of P from the soil solution may be needed for decomposition to progress (Gijssman et al., 1997). In contrast, late-seral grasses

Table 2
Pearson correlation coefficients (r) ($n = 15$) between mass loss and initial litter quality parameters

	Leaf litter	Roots
Lignin	-0.90***	-0.22 ^a
N	0.88***	0.55*
P	0.90***	0.71**
C:N	-0.89***	-0.62**
Lignin:N	-0.91***	-0.45 ^a
Lignin:P	-0.91***	-0.56*

^a $P > 0.05$.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

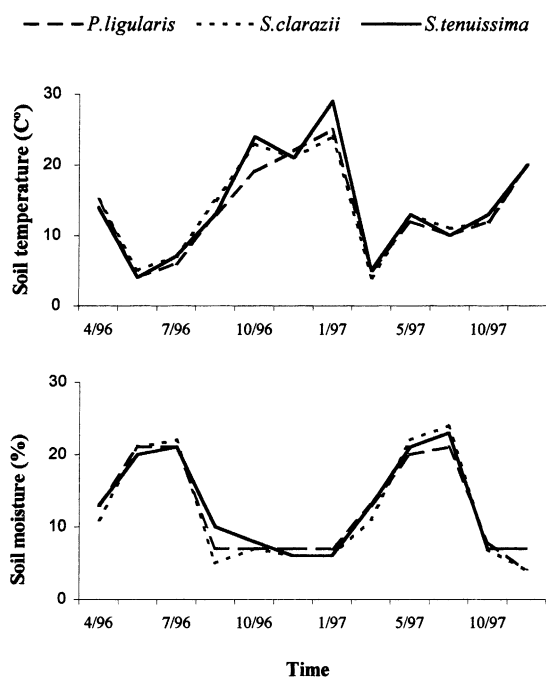


Fig. 3. Superficial soil (0–3 cm depth) temperature and percentage of soil (0–15 cm depth) moisture in *P. ligularis*, *S. clarazii* and *S. tenuissima*. Values are means of five samples.

from relatively humid environments have a high capacity to immobilize nutrients (Wedin, 1995). Wedin (1999) presented a conceptual model of the dependence of N availability on litter quality. It assumes that a C:N ratio of roughly 30 for plant litter represents the breakpoint above which there is net immobilization of N and below which there is net mineralization of N. In our study, the C:N ratio of the litter of all species was close to this threshold, except for the C:N ratio of the leaf litter of the unpalatable grass (C:N ratio of 48, Table 1). As predicted by the model, the greatest immobilization of N occurred in the leaf litter of the unpalatable species.

The capacity to immobilize nutrients of the species present in an ecosystem may have important implications with regards to plant community dynamics and stability (Wedin, 1999). The lower the capacity to buffer pulses of high nutrient availability (low capacity to immobilize nutrients), the higher the opportunity for plant species with high nutrient requirements to increase their abundance in the plant community. Pulses of high nutrient availability can be caused by

factors such as fire and drought (drought enhances the amount of detritus for decomposition and nutrient mineralization through increasing tissue mortality). In our study system, because the unpalatable grasses apparently have a low capacity to immobilize nutrients, pulses of high nutrient availability caused by fire and/or drought (historically recurrent in the system; Distel and Bóo, 1996) may have created opportunities for plant species with high resource requirements (palatable species) to maintain dominance within natural communities. Plants with high nutrient requirements commonly have higher rates of nutrient uptake and growth and, consequently, higher competitive ability (Grime, 1979). Previous results showed that the competitive ability of the palatable grasses is higher than that of the unpalatable grasses in the studied system (Moretto and Distel, 1997). Grazing is other factor that can also increase soil nutrient availability (McNaughton et al., 1988; McNaughton et al., 1997), and may, therefore, favor dominance of the palatable species. However, the high nutrient availability states induced by grazing may be unstable under heavy and continuous selective grazing by domestic animals, leading to reduced dominance of palatable species in favor of unpalatable species (Jefferies et al., 1994; Pastor and Cohen, 1997). Experimental evidence (Anderson and Briske, 1995; Moretto and Distel, 1999) supports the hypothesis that selective defoliation of the palatable species confers a competitive advantage to unpalatable species, which could ultimately lead to species replacement in grasslands.

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