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Soil nitrogen availability under grasses of different palatability in a temperate semi-arid rangeland of central Argentina

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Abstract Grazing by domestic livestock is frequently associated with the replacement of high-nutrient palatable species with low-nutrient unpalatable species, which may have a substantial effect on nutrient cycling. The objective of the present study was to compare soil N availability and net N mineralization in soils under *Poa ligularis* (palatable grass) with those in soils under *Stipa tenuissima* (unpalatable grass) in a temperate semi-arid rangeland of central Argentina. Nitrogen availability and net mineralization under laboratory and field conditions were measured. Soil N availability under *P. ligularis* was higher than or similar to soil N availability under *S. tenuissima. In situ* net N mineralization in the soil under *P. ligularis* was lower than or similar to net N mineralization in the soil under *S. tenuissima.* Potential net N mineralization was greater in the soil under *P. ligularis* than in the soil under *S. tenuissima.* Our results suggest that the replacement of palatable grasses by unpalatable grasses in the temperate semi-arid rangelands of central Argentina may imply a reduction in the rate of nutrient cycling.

Key words: Argentina, grasses, nitrogen mineralization, nutrient cycling, *Poa ligularis*, rangeland, species replacement, *Stipa tenuissima.*

INTRODUCTION

Soil N availability for plants at any point in time and space reflects the balance between the processes of: (i) mineralization from decomposing soil organic matter (newly added residues, existing degraded residues of varying age and degree of recalcitrance, and microbial biomass); (ii) immobilization in soil microbial biomass; (iii) plant uptake; (iv) depositions; and (v) losses (denitrification and leaching). The quality of the plant litter incorporated into soil organic matter has a substantial effect on mineralization and immobilization processes (Jarvis *et al.* 1996). High C : N ratios and lignin concentrations in litter commonly lead to N immobilization and hence low N availability, whereas low C : N ratios and lignin concentrations lead to N mineralization and high N availability. A C : N ratio of approximately 30 for plant litter appears to represent a threshold above which there is immobilization of N and below which it is mineralized (Aber & Melillo 1991).

In arid and semi-arid rangelands, late-seral dominant grasses commonly have low C : N ratios and lignin concentrations in both live and senesced tissues, which result in high palatability to ungulate grazers (i.e. they are consumed to a greater degree than expected based on their abundance) and net N mineralization (Wedin 1995, 1999). In the semi-arid rangelands of central Argentina, live and senesced tissues of palatable grasses are higher in N and have a lower C : N ratio and lignin concentration than those of unpalatable grasses (Moretto & Distel 1997; Moretto *et al.* 2001). Domestic livestock (cattle, sheep and goats) show a high degree of selection for palatable grasses and rejection of unpalatable grasses (Pisani *et al.* 2000), which is associated with a decrease in the abundance of the former and an increase in the abundance of the latter species in grazed areas (Llorens 1995; Distel & Bóo 1996). Therefore, if N mineralization is lower under unpalatable grasses than under palatable grasses, this shift in species composition may reduce soil N availability and slow down the rate of ecosystem nutrient cycling.

The objective of our study was to compare soil N availability and net N mineralization in soils under a palatable grass (*Poa ligularis*) with those in soils under an unpalatable grass (*Stipa tenuissima*) in a temperate semi-arid rangeland of central Argentina. Based on background information we expected to find a higher concentration of available soil N and net N mineralization in the soil under the palatable grass than in the soil under the unpalatable grass.

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METHODS

Study area

The research was conducted in the Caldén District (Cabrera 1976) on an upland area in the south-eastern zone of La Pampa province in central Argentina (63°45′W, 38°45′S; 80 m a.s.l.). The 20-ha study area had not been grazed by domestic animals (cattle, sheep or goats) for approximately 20 years. The climate is temperate and semi-arid. 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 400 mm, with peaks in October and March. Severe droughts occur during summer. Annual precipitation during the study period was 375 mm in 1998, 560 mm in 1999 and 369 mm in 2000. The vegetation is grassland with isolated woody plants (Distel & Bóo 1996). The most abundant species in the herbaceous layer are perennial C_3 cool-season bunchgrasses (Distel & Peláez 1985). The dominant grasses palatable for domestic livestock are *Stipa clarazii*, *Stipa tenuis*, *Poa ligularis* and *Piptochaetium napostaense*, but individuals and patches of the unpalatable grasses *Stipa gynerioides*, *Stipa tenuissima*, *Stipa trichotoma*, *Stipa speciosa* and *Stipa brachichaeta* are common. Recruitment of unpalatable grasses is rare, but once individuals are established they are highly persistent. The lignin and N concentrations and C : N ratios in live and senesced leaves and roots of *P. ligularis* and *S. tenuissima* are shown in Table 1. The dominant woody species are *Prosopis caldenia*, *Prosopis flexuosa*, *Larrea divaricata*, *Condalia microphilla* and *Chuquiraga erinacea*. The dominant soils are coarse-textured Calciustolls. A petrocalcic horizon is commonly found at depths of 60–80 cm. Soil properties under *P. ligularis* and *S. tenuissima* are shown in Table 2. Soil properties that can influence mineralization rates, such as soil drainage and soil compaction, were not measured in the present study. However, it can be reasonably assumed that there were no major differences in drainage and compaction between the soil under *P. ligularis* and *S. tenuissima* sampled in this study, because of their close proximity and the similarities in microtopography, texture and grazing history of the areas in which they were grown.

Table 1. Lignin, N and C : N ratio in two grass species, *Poa ligularis* (palatable) and *Stipa tenuissima* (unpalatable)

Plant part	*Poa ligularis*	*Stipa tenuissima*
Green leaves		
Lignin (%)	3.1 ± 0.1^a	8.1 ± 0.5^b
N (%)	2.1 ± 0.02^a	1.2 ± 0.06^b
C : N	22 ± 1.2^a	37 ± 0.9^b
Senesced leaves		
Lignin (%)	3.9 ± 0.09^a	7.9 ± 0.26^b
N (%)	1.6 ± 0.05^a	0.9 ± 0.01^b
C : N	26 ± 1.4^a	49 ± 0.5^b
Roots		
Lignin (%)	13.0 ± 0.50^a	19.0 ± 0.30^b
N (%)	1.1 ± 0.03^a	1.1 ± 0.04^a
C : N	35 ± 0.9^a	38 ± 0.5^b

Data are given as mean ± SE ($n = 10$). Different letters in a row indicate a significant difference ($P < 0.05$).

In situ soil incubations

In situ net N mineralization was periodically estimated by using the tube incubation technique (Raison *et al.* 1987) in the autumn (April–June) and spring (September–October) peaks of growing activity of 1998, 1999 and 2000. Soil samples were collected by using PVC tubes (15 cm long and 3.5 cm in diameter) under the canopy of 10 individuals of *P. ligularis* and 10 of *S. tenuissima*. Plants were randomly selected at each of 10 locations approximately 100 m from each other, where individuals of both species were interspersed. At each location, the distance between sampled plants varied from 1 to 10 m. New individuals were selected on each sampling occasion. For each sample we collected one soil core for initial analysis and left one in place for incubation for 30 days. In 1998 tubes contained intact uncovered soil cores, in 1999 tubes contained sieved (2-mm mesh) top-covered soil cores, and in 2000 the tubes contained intact top- and bottom-covered soil cores. Fresh soil samples were frozen immediately after collection and transported to the laboratory, where initial and incubated soil samples were analysed for inorganic N (NH_4^+ ± N and NO_3^-–N) by using the steam distillation technique (Bremner & Keeney 1965) after extraction with 2 M KCl. Concentrations were expressed on the basis of oven-dried (105°C) soil weight. Net N mineralization was calculated by subtracting initial NH_4^+ ± N plus NO_3^-–N concentrations from final concentrations.

Table 2. Soil properties under two grass species, *Poa ligularis* (palatable) and *Stipa tenuissima* (unpalatable)

Soil property	*Poa ligularis*	*Stipa tenuissima*
C (%)	1.4 ± 0.07^a	1.4 ± 0.08^a
N (%)	0.17 ± 0.07^a	0.13 ± 0.004^b
C : N	8.5 ± 0.23^a	11.0 ± 0.7^b
P (p.p.m)	20.1 ± 1.6^a	9.8 ± 1.1^b
pH	7.6 ± 0.3^a	7.7 ± 0.5^a
Sand (%)	62.0 ± 1.0^a	63.0 ± 1.8^a
Silt (%)	26.5 ± 1.0^a	26.0 ± 0.9^a
Clay (%)	11.5 ± 0.5^a	11.0 ± 1.3^a

Data are given as mean ± SE ($n = 10$). Different letters in a row indicate a significant difference ($P < 0.05$).

Nitrogen availability corresponded to the inorganic N content in the initial samples.

Laboratory soil incubations

In the autumn and spring of 2000, soil samples from 0 to 15 cm depth were collected under the canopy of 10 different individuals of *P. ligularis* and 10 of *S. tenuissima* from the same locations where *in situ* net N mineralization was measured, and incubated in the laboratory to estimate potential net N mineralization. Plastic pots of 250-mL capacity were filled with 50 g previously sieved (2-mm mesh) fresh soil samples and incubated for 1, 2, 4, 6, 8, 12 and 16 weeks at 25°C and 20% soil moisture. There were 10 replicates per species and period of incubation. Potential net N mineralization for each incubation period was determined as for the incubated *in situ* soil, as described previously.

Plant properties

Green leaves and recently senesced leaves and roots from *P. ligularis* and *S. tenuissima* collected at the study area were analysed for C, N and lignin. Carbon was determined by dry combustion with an elemental analyser (Leco, model CR-1). Nitrogen was

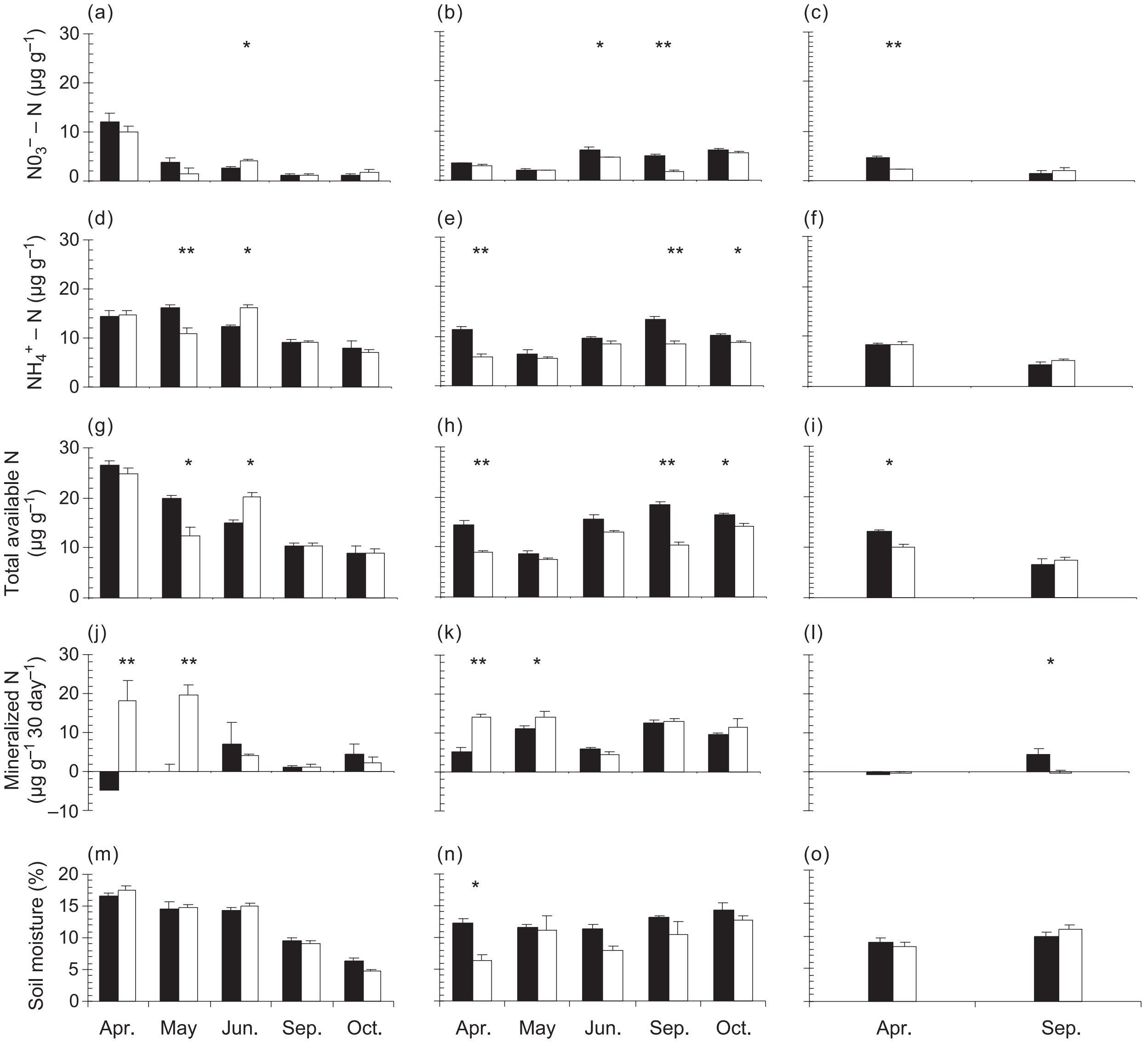

Fig. 1. *In situ* soil (0–15 cm) measurements of available N as NH_4^+–N plus NO_3^-–N, net N mineralization, and soil moisture under two grass species, (■) *Poa ligularis* (palatable) and (□) *Stipa tenuissima* (unpalatable). (a,d,g,j,m) 1998; (b,e,h,k,n) 1999; (c,f,i,l,o) 2000. Data are given as mean ± SE ($n = 10$). For each date, significant differences are shown at $*P < 0.05$, and $**P < 0.01$.

determined by using the semimicro Kjeldahl technique, and lignin was determined by using the detergent method (Goering & Van Soest 1970).

Soil properties

In April 2000 new soil samples ($n = 10$) were collected under the canopy of both *P. ligularis* and *S. tenuissima* from the same locations where *in situ* net N mineralization was measured, and analysed for total organic C by dry combustion with an elemental analyser, for total N by using the semimicro Kjeldahl technique, and for extractable P according to Bray and Kurtz 1945). Soil texture was determined by using the pipette method (Green 1981).

Statistical analysis

Data were analysed by using Student's *t*-test to determine the significance of the differences between several physical and chemical variables of the soil under the canopies of *P. ligularis* and *S. tenuissima.* Measurements on each date were analysed separately.

RESULTS

Green and senesced leaves of the palatable grass (*P. ligularis*) were higher in N ($P < 0.05$) and lower in lignin ($P < 0.05$) and had a lower C : N ratio than leaves of the unpalatable grass (*S. tenuissima*; Table 1). The roots of *P. ligularis* were also lower in lignin ($P < 0.05$) and had a lower C : N ratio than *S. tenuissima*, but they had similar N concentrations. Both species differed more in leaf chemistry than in root chemistry. In April 2000, concentrations of both total N and extractable P were higher ($P < 0.05$) and the C : N ratio was lower ($P < 0.05$) in the soil under *P. ligularis* than in the soil under *S. tenuissima* (Table 2). None of total organic carbon concentration, pH or texture differed significantly between the soils associated with the two species ($P > 0.05$). Except for one date (April 1999), soil water content did not differ significantly between soils under either species ($P > 0.05$; Fig. 1).

Soil N availability under *P. ligularis* was higher than ($P < 0.05$) or similar to ($P > 0.05$) soil N availability under *S. tenuissima*, except in June 1998 (Fig. 1). In both species, there was more nitrogen available in the form of $NH_4^+ \pm N$ than in the form of NO_3^-–N. *In situ* net N mineralization in the soil under *P. ligularis* was lower than ($P < 0.05$) or similar to ($P > 0.05$) net N mineralization in the soil under *S. tenuissima*, except in September 2000 (Fig. 1). In contrast, potential net N mineralization measured under laboratory conditions was higher in the soil collected under *P. ligularis* than in the soil under *S. tenuissima* in both April and September 2000 ($P < 0.05$; Fig. 2).

DISCUSSION

Our results support the hypothesis that soil N availability is higher in the soil under the palatable grass *P. ligularis* than in the soil under the unpalatable grass *S. tenuissima* (Fig. 1). The availability of N was normally the same or higher under the palatable species than under the unpalatable species in autumn and spring, when both species have their peaks of growing activity and nutrient utilization (Distel & Peláez 1985). These results are particularly significant, considering that N concentration in green leaves, and presumably depletion of soil N, was higher in *P. ligularis* than in *S. tenuissima* (Table 1). The availability of N mainly in the form of NH_4^+–N is common in natural grasslands because nitrification is inhibited by water shortage (Kovda *et al.* 1979) and/or allelopathic compounds produced by late successional bunchgrasses (Rice 1984). There were also higher concentrations of total N and extractable P, and lower C : N ratios in the soil under *P. ligularis* than in the soil under *S. tenuissima* (Table 2). The results for available N were consistent with the higher potential net N mineralization under *P. ligularis* than under *S. tenuissima* derived from laboratory incubations (Fig. 2). The results did not agree with *in situ* estimates of net N mineralization (Fig. 1). Field net N mineralization was more frequently higher under the unpalatable

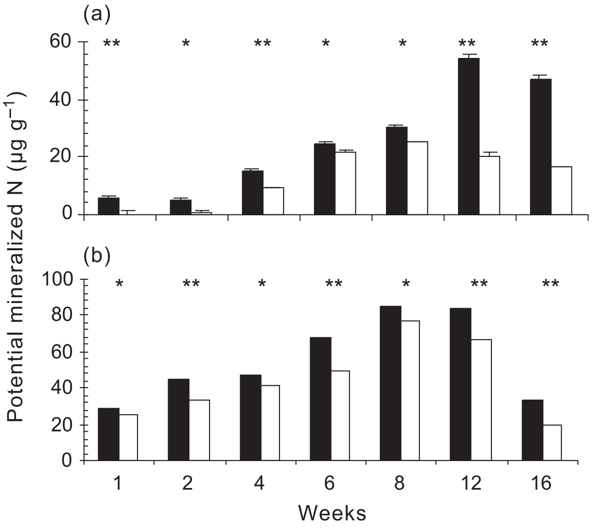

Fig. 2. Soil potential net N mineralization under two grass species, (■) *Poa ligularis* (palatable) and (□) *Stipa tenuissima* (unpalatable). (a) April; (b) September. Data are given as mean ± SE ($n = 10$). At each date, significant differences are shown at *$P < 0.05$, and **$P < 0.01$.

species *S. tenuissima* than under the palatable species *P. ligularis* during the experimental period. However, problems associated with *in situ* incubations may have influenced the results and made them difficult to interpret.

In situ incubations involve artefacts that can bias estimates of net N mineralization (Binkley & Vitousek 1991; Hook & Burke 1995). In intact cores (used in 1998 and 2000), root death may temporarily increase N immobilization. The importance of this artificially enhanced immobilization may depend strongly on root density and on duration of the incubation. Hook and Burke (1995) recommended using 15–30-day incubations of intact cores to minimize artefacts and we used 30-day incubation periods. Alternatively, sieved cores (used in 1999) prevent N immobilization, but sieving can artificially enhance mineralization through overexposing soil organic matter to microbial attack (Raison *et al.* 1987). However, open cores (used in 1998) have the advantage of tracking natural soil water regimes, but they may bias estimates of net N mineralization rates because of external depositions and/or leaching. In conclusion, assuming that a 30-day incubation period was short enough to reduce N immobilization in severed roots, the more suitable incubation technique for interspecific comparisons was probably the incubation using intact top- and bottom-covered cores (used in 2000). Results from 2000 show higher or equal mineralization under *P. ligularis*, as in the laboratory incubations.

Recent research (Moretto *et al.* 2001) has found significant differences between *P. ligularis* and *S. tenuissima* in leaf litter decay rate and net N release, and no significant differences between them in root decay rate and net N release. This finding is relevant because roots represent the major input of new soil organic matter in the semi-arid rangelands of central Argentina (Distel & Fernández 1986). However, the effect of plant species on nutrient cycling is determined by both the nutrient release rate from soil organic matter and the total amount of litter (both above- and below-ground) that is produced and incorporated into soil organic matter per unit of ground area (Chapin 1991). Preliminary results suggest that litter production is higher in *P. ligularis* than in *S. tenuissima* (A. Flemmer, unpubl. data). Interspecific differences in the production of litter may therefore help to explain the pattern of soil N availability. The largest differences between these species in soil N availability occurred in 1999, coinciding with more rainfall and, supposedly, more litter production in the palatable species.

Our results suggest that the replacement of palatable grasses by unpalatable grasses in the semi-arid rangelands of central Argentina may be associated with a reduction in the rate of nutrient cycling. Unpalatable species commonly have relatively low potential productivity, turnover rates and/or nutrient release rates (Aerts & Chapin 2000). The limitations in nutrient supply imposed by unpalatable species may represent a positive feedback, because these species are adapted to a shortage of nutrients (Aerts & Chapin 2000). This type of positive feedback has recently been described by several authors (Berendse 1994; Jones *et al.* 1994; Aerts 1995). However, compared with unpalatable C_4 grasses from humid grasslands (Wedin 1995) or mixtures of C_3 and C_4 grasses from cold semi-arid grasslands with high concentrations of soil organic carbon (Barrett & Burke 2000), our results suggest that unpalatable C_3 grasses from the temperate semi-arid grasslands of central Argentina have a relatively low potential to immobilize nutrients. If so, pulses of high nutrient availability (caused by fertilizer application, fire, drought, etc.) may create opportunities for plant species with high resource requirements (palatable species) to realize a competitive advantage and maintain or gain dominance within natural grassland communities (Wedin 1999).

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