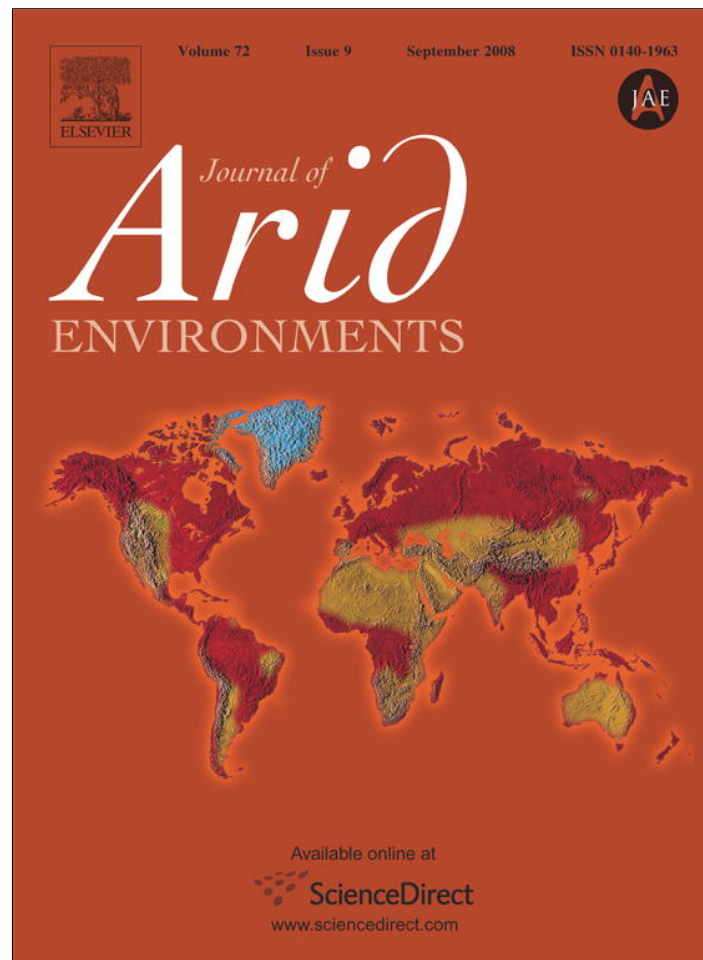


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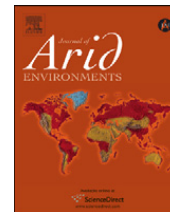
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# Litter quality of C<sub>3</sub> perennial grasses and soil inorganic nitrogen in a semiarid rangeland of central Argentina <sup>☆</sup>

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## ABSTRACT

The study was undertaken to quantify litter quality of six C<sub>3</sub> perennial grasses and species effects on soil inorganic nitrogen (N) in a semiarid rangeland of central Argentina. Leaf litter and roots were analyzed for N, carbon, phosphorus and lignin concentrations. Field measurements and laboratory experiments compared inorganic N content and potential net N mineralization in the soil under selected grasses. Species were represented by two palatable late-seral grasses (*Poa ligularis* and *Stipa clarazii*), two unpalatable late-seral grasses that increase in abundance under heavy grazing (*Stipa ambigua* and *Stipa gynerioides*) and two palatable mid-seral grasses (*Piptochaetium napostaense* and *Stipa tenuis*). Species exhibited relatively little variation in the chemical composition of leaf litter and roots. The soils associated with these species did not differ in inorganic N content in field or potential net N mineralization. Furthermore, amending soils with roots of these species had no consistent impact on inorganic N content. Our results suggest C<sub>3</sub> perennial grasses that differ in their palatability to grazers do not differentially influence soil inorganic N dynamic in semiarid rangelands of central Argentina.

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## 1. Introduction

For a given combination of inputs, losses and plant uptake, soil inorganic nitrogen (hereafter inorganic N) content reflects in large part the balance between the processes of mineralization and immobilization by soil microbial biomass (Aber and Melillo, 1991; Killham, 1995; Knops et al., 2002). Plant litter quality exerts an important positive feedback on N dynamic by controlling the balance between both processes (Hobbie, 1992; Wedin, 1999). This positive feedback consists in higher litter quality leading to faster decomposition and net N mineralization, and in lower litter quality leading to slower decomposition and net N immobilization (Aerts and Chapin, 2000; Pastor et al., 1984; Vitousek, 1982).

In semiarid rangelands of central Argentina, changes in species composition induced by grazing of domestic livestock include the replacement of palatable late-seral and mid-seral grasses by unpalatable late-seral grasses (Distel and Bóo, 1996; Llorens, 1995). Species in the first two groups are higher in protein and lower in structural carbohydrates than species in the latter group (Cerqueira et al., 2004; Distel et al., 2005; Moretto and Distel, 1997). Species less palatable to livestock should also lower litter quality; and lowering of litter quality should cause unpalatable species to influence soil inorganic N levels in ways different from palatable species. However, in the studied system both palatable and unpalatable grasses conform to C<sub>3</sub> photosynthetic pathway (Distel and Peláez, 1985) and, within a single functional group, variation in plant tissue chemistry is limited relative to that between groups (e.g., C<sub>3</sub> vs. C<sub>4</sub> grasses) (Moretto and Distel, 2003; Moretto

<sup>☆</sup> All plant species nomenclature follows Rógolo de Agrasar et al. (2005).

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et al., 2001; Semmartin et al., 2004; Wedin, 1995; Wedin and Tilman, 1990; Wedin and Pastor, 1993). Hence, limited variation in litter quality may reduce differences among species in their effects on soil inorganic N in these rangelands. In the present study, we compared six C<sub>3</sub> perennial grasses in their effect on inorganic N dynamic: *Stipa clarazii*, *Poa ligularis*, *Stipa gynerioides*, *Stipa ambigua*, *Piptochaetium napostaense* and *Stipa tenuis*. The first two species are representative of palatable late-seral grasses, the following two are representative of unpalatable late-seral grasses that increases in abundance under heavy grazing, and the latter two species are representative of palatable mid-seral grasses (Distel and Bóo, 1996). Our specific objective was to quantify the amount of variation in litter quality among C<sub>3</sub> selected grasses and to investigate to what extent this variation is translated into species differences in (1) soil inorganic N content in the field, (2) soil potential net N mineralization, and (3) inorganic N content in soil amended with roots under laboratory conditions.

## 2. Materials and methods

### 2.1. Study site

The study was conducted in the Caldén District (Cabrerá, 1976), on an upland site (2 ha) located in the south-eastern zone of La Pampa province in central Argentina (39°12'S; 63°41'W). The site has been excluded from livestock grazing since three years before the beginning of the study. Before that, it had been under continuous, heavy grazing by sheep and cattle. The climate of the region is temperate and semiarid (Instituto Nacional de Tecnología Agropecuaria et al., 1980). 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 March and October. Mean annual potential evapotranspiration is 800 mm. Annual precipitation during the study period was 379 mm in 2002 and 365 mm in 2003. The dominant soils are coarse-textured petrocalcic calciustolls (Castelli et al., 1995), with a petrocalcic horizon typically at 60–80 cm depth. Physiognomy is grassland dominated by C<sub>3</sub>, perennial, cool-season grasses with isolated woody plants (Distel and Peláez, 1985).

### 2.2. Leaf litter and root chemical composition

Leaf material that had recently senesced and that was still connected to the plant, and roots still attached to the crown after removing the soil by gently washing with tap water were collected ( $n = 10$  plants) at the end of their annual growing cycle (December 2002). Leaves and roots were dried at 60 °C to constant mass, ground to pass a 40 mesh sieve, and analyzed for N (micro-Kjeldahl procedure; Bremner and Mulvaney, 1982), C (dry combustion; LECO CR12), lignin (Detergent Method; Goering and Van Soest, 1970) and phosphorus (atomic spectrometry; Sequential Plasma Spectrometer Shimadzu ICPS 1000-III). Subsamples of leaf litter and roots were incinerated at 550 °C for 3 h to determine ash content, which allowed the expression of chemical parameters on an ash-free dry matter basis.

### 2.3. Soil inorganic N content

Soil cores (3 cm diameter  $\times$  10 cm deep) were collected directly under the canopy of 10 randomly located plants of *P. ligularis*, *P. napostaense*, *S. ambigua*, *S. clarazii* and *S. gynerioides* in September, November and December of 2002. New individuals were selected on each sampling occasion. Soil samples were immediately cooled with ice, and taken to the laboratory (approximate transport time was 4 h), sieved to separate plant material and soil fragments  $> 2$  mm in diameter, and submerged (10 g subsample) into 50 mL of 2 M KCl for 24 h to extract inorganic N. The extracts were filtered and analyzed by steam distillation with MgO and Devarda's alloy to determine NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup> content (Keeney and Nelson, 1982). An additional subsample (20 g) was oven-dried at 105 °C for 48 h to determine the water content and to express inorganic N content (NH<sub>4</sub><sup>+</sup>+NO<sub>3</sub><sup>-</sup>) on dry soil mass basis. This procedure was repeated in May, July, September and November of 2003 and January of 2004 ( $n = 15$  plants per species per date), except that soil was collected under the canopies of *P. ligularis*, *S. ambigua*, *S. gynerioides* and *S. tenuis*.

### 2.4. Potential net N mineralization

In May, July, September and November of 2003 soil cores (3 cm diameter  $\times$  10 cm deep) were collected directly under the canopy of 15 randomly located plants of *P. ligularis*, *S. ambigua*, *S. gynerioides* and *S. tenuis*. New individuals were selected on each sampling occasion. Once in the laboratory, each sample was passed through a 2 mm sieve and then divided into two subsamples. One subsample was used to estimate initial inorganic N content and the other used for soil incubation. Plastic pots (250 mL capacity) were filled with 50 g of soil and incubated for 60 days at 25 °C and 15% soil gravimetric water content (80% water holding capacity). The level of soil water content was maintained by weighing the pots once a week and adding the necessary amount of water. Potential net N mineralization (hereafter 'N mineralization' is abbreviated to 'Nmin') was calculated by subtracting the initial inorganic N content from the final inorganic N content. Concentrations of NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup> were determined as described in Section 2.3.

## 2.5. Inorganic N content in soils amended with roots

Two hundred and forty plastic pots (250 mL capacity) were filled with 100 g of air-dried, carefully mixed and sieved (to remove roots and litter fragments larger than 2 mm) soil, collected randomly between grass plants (0–10 cm depth). Pots were then randomly assigned to four treatments and six sampling dates (10 replicates each). The treatments consisted in the addition of 0.5 g of roots (obtained as described in 2.2) of *P. ligularis*, *S. tenuis* or *S. gynerioides*. Root–soil proportion (0.5 g of roots per 100 g soil) was based on relations observed in the field. There was also a control treatment with no addition of roots. Experimental units were then incubated for 15, 30, 45, 60, 75 and 90 days at 25 °C and 15% gravimetric water content (80% water holding capacity). Inorganic N content was measured at the beginning of the experiment and at the end of each incubation period as described in Section 2.3.

## 2.6. Statistical analysis

Litter chemical composition, soil inorganic N content and potential net Nmin were analyzed by one-way analysis of variance (ANOVA) to test for species effect. Each plant part (leaf litter or root), sample date or period of incubation was analyzed separately. When species effect was not significant, we performed power analyses to determine the probability of being right in accepting the null hypothesis (Sall et al., 2001). Data on inorganic N content in soils incubated with or without root amendments were analyzed by two-way ANOVA to test for the treatment and time effects. Transformed data were used when necessary to satisfy the assumptions of the ANOVA. A Tukey's test was performed when results of ANOVA were significant. Leaf litter and root chemical composition of species groups (palatable late-seral grasses, unpalatable late-seral grasses and palatable mid-seral grasses) were compared by orthogonal contrast. We considered statistical probabilities of  $p < 0.05$  as significant in all the tests.

## 3. Results and discussion

### 3.1. Leaf litter and root chemical composition

There were differences among species in all chemical traits for both leaf litter and roots (Table 1), although variations were not consistent when considering all the chemical parameters. Root litter chemistry was quite similar to leaf litter chemistry, except for the higher lignin concentration in the former than in the latter tissues. A similar result was found at species group level (palatable late-seral grasses, unpalatable late-seral grasses and palatable mid-seral grasses; data not shown). The observed variations among C<sub>3</sub> perennial grass species were relatively low compared to variations observed between C<sub>3</sub> and C<sub>4</sub> grasses (Gijsman et al., 1997; Urquiaga et al., 1998; Wedin and Tilman, 1990; ). For example, the C:N ratio in leaf litter (110) and roots (100) of *Schyzachyrium scoparium* (C<sub>4</sub> grass) is well above the range in C:N ratio in leaf litter (40–62) and roots (34–59) observed in this study (Wedin and Tilman, 1990). Even though palatable and unpalatable C<sub>3</sub> grasses show large differences in aboveground green tissue chemistry (Cerqueira et al., 2004; Distel et al., 2005), they exhibited relatively little variation in the chemical composition of leaf litter and roots.

**Table 1**  
Mean ( $\pm$ S.E.;  $n = 10$ ) chemical composition of ash-free leaf litter and roots

	C (g kg organic matter <sup>-1</sup> )	N (g kg organic matter <sup>-1</sup> )	C:N	P (g kg organic matter <sup>-1</sup> )	Lignin (g kg organic matter <sup>-1</sup> )
<b>Leaf litter</b>					
<i>Poa ligularis</i>	404.0 $\pm$ 1.7 a	6.7 $\pm$ 0.4 a	61.6 $\pm$ 3.5 b	0.6 $\pm$ 0.02 ab	28.9 $\pm$ 1.1 b
<i>Piptochaetium napostaense</i>	406.7 $\pm$ 3.2 a	9.9 $\pm$ 0.8 b	43.3 $\pm$ 3.2 a	0.9 $\pm$ 0.07 b	31.5 $\pm$ 6.5 b
<i>Stipa ambigua</i>	404.9 $\pm$ 2.5 a	10.7 $\pm$ 0.8 b	40.1 $\pm$ 3.3 a	0.9 $\pm$ 0.04 b	75.3 $\pm$ 2.8 c
<i>Stipa clarazii</i>	397.9 $\pm$ 3.8 a	8.4 $\pm$ 0.6 ab	50.0 $\pm$ 4.4 ab	0.8 $\pm$ 0.03 b	45.1 $\pm$ 4.2 b
<i>Stipa gynerioides</i>	406.8 $\pm$ 2.6 a	6.9 $\pm$ 0.2 a	59.5 $\pm$ 1.9	0.5 $\pm$ 0.04 a	82.5 $\pm$ 9.7 c
<i>Stipa tenuis</i>	469.4 $\pm$ 3.3 b	8.4 $\pm$ 0.4 ab	56.9 $\pm$ 2.6 b	0.6 $\pm$ 0.04 ab	14.6 $\pm$ 3.9 a
<i>P</i>	<0.0001	<0.0001	<0.0001	0.0043	<0.0001
<b>Roots</b>					
<i>Poa ligularis</i>	396.9 $\pm$ 7.0 ab	8.5 $\pm$ 0.6 ab	48.3 $\pm$ 3.6 bc	0.6 $\pm$ 0.02 ab	109.0 $\pm$ 6.4 a
<i>Piptochaetium napostaense</i>	412.0 $\pm$ 4.9 ab	12.5 $\pm$ 0.8 c	34.1 $\pm$ 2.0 a	0.8 $\pm$ 0.07 b	102.5 $\pm$ 6.6 a
<i>Stipa ambigua</i>	415.8 $\pm$ 6.2 b	11.3 $\pm$ 0.9 bc	39.0 $\pm$ 3.0 ab	0.8 $\pm$ 0.04 b	166.5 $\pm$ 18.0 bc
<i>Stipa clarazii</i>	394.1 $\pm$ 3.0 a	7.6 $\pm$ 0.2 a	52.3 $\pm$ 1.3 c	0.7 $\pm$ 0.03 b	126.7 $\pm$ 4.8 ab
<i>Stipa gynerioides</i>	415.7 $\pm$ 1.7 b	7.5 $\pm$ 0.7 a	59.0 $\pm$ 3.9 c	0.4 $\pm$ 0.04 a	196.6 $\pm$ 8.0 c
<i>Stipa tenuis</i>	488.3 $\pm$ 4.9 c	11.4 $\pm$ 1.1 bc	46.1 $\pm$ 4.1 abc	0.8 $\pm$ 0.04 b	107.2 $\pm$ 6.1 a
<i>P</i>	<0.0001	<0.0001	<0.0001	0.0004	<0.0001

Values within a column and plant part followed by different letters were significantly different (Tukey test,  $p < 0.05$ ).

### 3.2. Soil inorganic N

Inorganic N content of soils under the canopies of the studied species was similar at all the measurement dates, except for November of 2003, when it was lowest in the soil under *P. ligularis* (Table 2). Power analyses indicated that the probability of detecting differences among species in soil inorganic N content was moderated to high (65–85%).

Potential net Nmin of soils associated with canopies of the studied species was similar, except in November of 2003, when it was the highest in soils under *P. ligularis* canopy (Table 3). Power analyses indicated that the probability of detecting differences among species in potential net Nmin was moderated to high (70–85%).

The low inorganic N content and high potential net Nmin in soils associated with *P. ligularis* in November of 2003 may be related to the earlier maturation of this species (Distel and Peláez, 1985). Root decay toward the end of the annual growing cycle (Distel and Fernández, 1988) may have caused some immobilization of inorganic N by the soil microbial community under the canopy of *P. ligularis*, thereby lowering inorganic N content (Table 2). This immobilized N may have in part been mineralized during the 60-day incubation period, resulting in the high potential net Nmin observed for this species in November of 2003 (Table 3).

Inorganic N content in soils incubated with or without the addition of roots was affected by treatment ( $p < 0.0001$ ) and time ( $p < 0.0001$ ) of incubation (Fig. 1). On average, inorganic N content increased from  $7.6 \mu\text{g kg soil}^{-1}$  on day 0 to  $26.7 \mu\text{g kg soil}^{-1}$  on day 90. The treatment by time interaction was also significant ( $p < 0.01$ ). Inorganic N content in the soil with no addition of roots (control) was comparable to or higher than that in soils with root amendments, whereas inorganic N content in the soil incubated with roots of *S. gynerioides* was similar to or higher than inorganic N content in soils incubated with roots of *P. ligularis* or *S. tenuis*.

The consistently lower inorganic N content in the soil amended with roots of *P. ligularis* and *S. tenuis* during the first 75 days of incubation may reflect their faster root decomposition and an associated immobilization of inorganic N by the soil microbial community (Moretto and Distel, 2003). However, by day 90 of incubation, there was no difference in inorganic N content among soils amended with roots, regardless of species. The observed mineralization of N and the inconsistent

**Table 2**

Mean ( $\pm$ S.E.;  $n = 10$  in 2002,  $n = 15$  in 2003) inorganic N ( $\text{NH}_4^+ + \text{NO}_3^-$ ) content of soils under perennial  $\text{C}_3$  grasses

2002 Species	Inorganic N content ( $\mu\text{g kg soil}^{-1}$ )		
	September	November	December
<i>Poa ligularis</i>	16.0 $\pm$ 2.4	7.2 $\pm$ 1.4	5.3 $\pm$ 1.0
<i>Piptochaetium napostaense</i>	17.2 $\pm$ 2.8	9.2 $\pm$ 1.6	7.0 $\pm$ 1.2
<i>Stipa ambigua</i>	28.0 $\pm$ 5.1	7.0 $\pm$ 1.5	9.8 $\pm$ 1.8
<i>Stipa clarazii</i>	21.2 $\pm$ 1.6	6.7 $\pm$ 1.6	6.5 $\pm$ 0.9
<i>Stipa gynerioides</i>	20.5 $\pm$ 2.6	5.9 $\pm$ 1.1	7.4 $\pm$ 1.4
P	0.0789	0.5596	0.1811

2003 Species	Inorganic N content ( $\mu\text{g kg soil}^{-1}$ )				
	May	July	September	November	January
<i>Poa ligularis</i>	12.2 $\pm$ 1.4	12.5 $\pm$ 1.6	5.4 $\pm$ 0.7	3.6 $\pm$ 0.5 a	3.4 $\pm$ 0.7
<i>Stipa ambigua</i>	16.2 $\pm$ 1.2	11.3 $\pm$ 0.9	6.7 $\pm$ 0.7	7.2 $\pm$ 1.0 b	5.3 $\pm$ 0.7
<i>Stipa gynerioides</i>	12.2 $\pm$ 1.2	11.6 $\pm$ 0.9	5.8 $\pm$ 0.6	8.2 $\pm$ 1.1 b	4.2 $\pm$ 0.9
<i>Stipa tenuis</i>	13.3 $\pm$ 1.5	13.3 $\pm$ 1.4	6.5 $\pm$ 0.6	6.7 $\pm$ 0.9 ab	5.8 $\pm$ 1.3
P	0.1252	0.6242	0.4505	0.0063	0.2866

Values within a column and year followed by different letters were significantly different (Tukey test,  $p < 0.05$ ).

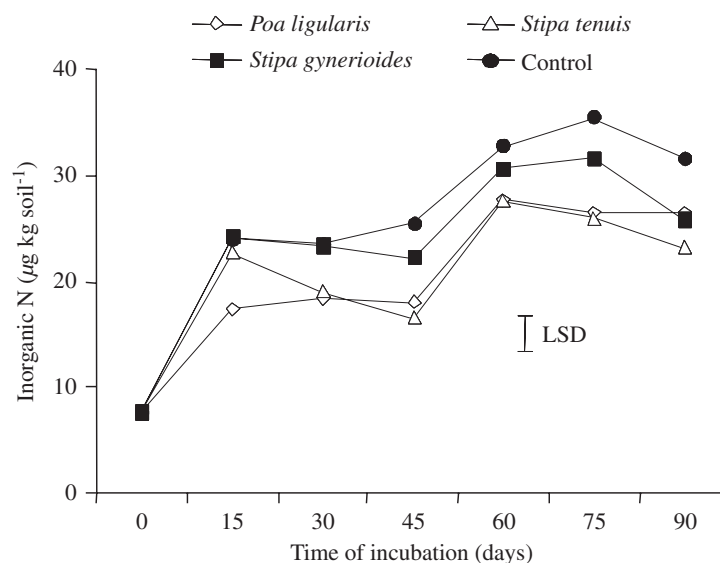
**Table 3**

Mean ( $\pm$ S.E.;  $n = 15$ ) potential net N mineralization ( $\text{NH}_4^+ + \text{NO}_3^-$ ) in soils associated with perennial  $\text{C}_3$  grasses and incubated in the laboratory for 60 days

Species	Net N mineralization ( $\mu\text{g kg soil}^{-1} 60 \text{ days}^{-1}$ )			
	May	July	September	November
<i>Poa ligularis</i>	19.6 $\pm$ 1.0	13.3 $\pm$ 2.2	33.8 $\pm$ 2.5	33.2 $\pm$ 3.1 b
<i>Stipa ambigua</i>	23.2 $\pm$ 2.5	17.8 $\pm$ 2.4	30.7 $\pm$ 2.4	28.6 $\pm$ 2.5 ab
<i>Stipa gynerioides</i>	17.3 $\pm$ 2.0	16.9 $\pm$ 1.7	30.9 $\pm$ 2.0	20.9 $\pm$ 1.8 a
<i>Stipa tenuis</i>	17.8 $\pm$ 2.3	15.8 $\pm$ 2.3	30.5 $\pm$ 1.6	23.9 $\pm$ 2.2 a
P	0.1796	0.5110	0.6647	0.0044

Initial values of inorganic N content for each species and date are in Table 2 (May, July, September, and November, 2003).

Values within a column followed by different letters were significantly different (Tukey test,  $p < 0.05$ ).



**Fig. 1.** Mean ( $n = 10$ ) cumulative net N mineralization in soils incubated with or without (control) the addition of roots of  $C_3$  perennial grass species. Vertical segment LSD represents the least significant difference ( $p < 0.05$ ) among treatments for the same sample date.

differences among species in root amended soils were in agreement with results from a microcosm experiment involving  $C_3$  grasses promoted and diminished by grazing (Semmartin et al., 2004).

Our results were in general agreement with the initial supposition of minimal differences among  $C_3$  perennial grasses in their effects on soil inorganic N in semiarid rangelands of central Argentina. Reduced variation in litter quality may explain the lack of differences among species in their effect on inorganic N dynamics. Previous studies at the same site involving palatable late-seral grasses (*P. ligularis*, *S. clarazii*) and unpalatable late-seral grasses (*S. tenuissima*, *S. gynerioides*), found similar rates of N release from decomposing roots (Moretto et al., 2001), and similar or inconsistent differences in net Nmin (Moretto and Distel, 2002). In another study at the same site, N release from decomposing roots proceeded faster in *P. ligularis* than in *S. gynerioides* for the first 120 days of incubation, but it was similar between species thereafter (Moretto and Distel, 2003).

#### 4. Implications

In semiarid rangelands of central Argentina palatable late-seral grasses are characterized by their high nutritive value (Cerqueira et al., 2004; Distel et al., 2005; Moretto and Distel, 1997), which results in marked livestock preference for them (Bontti et al., 1999; Bóo et al., 1993; Pisani et al., 2000). Heavy grazing reduces dominance of these grasses and favors mid-seral and unpalatable late-seral grasses (Distel and Bóo, 1996; Gallego et al., 2004; Llorens, 1995). However, because of limited variation in litter chemistry among species, the impact of these grazing-induced species replacement on ecosystem N cycling may be realized via effects on litter quantity rather than on litter quality.

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#### References

- Aber, J.D., Melillo, J.M., 1991. Terrestrial Ecosystems. Saunder College Publishing, Philadelphia.
- Aerts, R., Chapin III, F.S., 2000. The mineral nutrition of wild plants revisited: a reevaluation of processes and patterns. *Advances in Ecological Research* 30, 1–67.
- Bontti, E.E., Bóo, R.M., Lindström, L.I., Elía, O.R., 1999. Botanical composition of cattle and vizcacha diets in central Argentina. *Journal of Range Management* 52, 370–377.
- Bóo, R.M., Lindström, L.I., Elía, O.R., Mayor, M.D., 1993. Botanical composition and seasonal trends of cattle diets in central Argentina. *Journal of Range Management* 46, 479–482.
- Bremner, J.M., Mulvaney, C.S., 1982. Total nitrogen. In: Page, A.L., Miller, R.H., Keeney, D.R. (Eds.), *Methods of Soil Analysis, Part 2, Chemical and Microbiological Properties*. American Society of Agronomy, Madison, pp. 595–622.
- Cabrera, A., 1976. Regiones Fitogeográficas Argentinas. Acme, Buenos Aires.

- Castelli, L.M., Lázzari, A., Landricini, M.R., Miglierina, A.M., 1995. Características químicas de un suelo superficial del sur del Caldenal (Provincia de La Pampa, Argentina). *Ciencia del Suelo* 13, 44–46.
- Cerqueira, E.D., Sáenz, A.M., Rabortnikof, C.M., 2004. Seasonal nutritive value of native grasses of Argentina Calden forest range. *Journal of Arid Environments* 59, 645–656.
- Distel, R.A., Peláez, D.V., 1985. Fenología de algunas especies del Distrito del Caldén (*Prosopis caldenia* burk). *IDIA Sept-Dic*, 35–40.
- Distel, R.A., Fernández, O.A., 1988. Dynamics of root growth and decay in two grasses native to semiarid Argentina. *Australian Journal of Ecology* 13, 327–336.
- Distel, R.A., Bóo, R.M., 1996. Vegetation states and transitions in temperate semiarid rangelands of Argentina. In: West, N. (Ed.), *Rangelands in a Sustainable Biosphere*. Society for Range Management, Denver, pp. 117–118.
- Distel, R.A., Didoné, N.G., Moretto, A.S., 2005. Variations in chemical composition associated with tissue ageing in palatable and unpalatable grasses native to central Argentina. *Journal of Arid Environments* 62, 351–357.
- Gallego, L., Distel, R.A., Camina, R., Rodríguez Iglesias, R.M., 2004. Soil phytoliths as evidence for species replacement in grazed rangelands of central Argentina. *Ecography* 27, 725–732.
- Gijsman, A.J., Alarcón, H.F., Thomas, R.J., 1997. Root decomposition in tropical grasses and legumes, as affected by soil texture and season. *Soil Biology and Biochemistry* 29, 1443–1450.
- Goering, H.K., Van Soest, P.J., 1970. Forage Fiber Analyses, *Agronomy Handbook No. 379*. ARS USDA, Denver.
- Hobbie, S.E., 1992. Effects of plant species on nutrient cycling. *Trends in Ecology and Evolution* 7, 336–339.
- Instituto Nacional de Tecnología Agropecuaria, Provincia de La Pampa, Universidad Nacional de La Pampa, 1980. *Inventario Integrado de los Recursos Naturales de la Provincia de La Pampa*. INTA, Buenos Aires.
- Keeney, D.R., Nelson, D.W., 1982. Nitrogen inorganic forms. In: Page, A.L., Miller, R.H., Keeney, D.R. (Eds.), *Methods of Soil Analysis, Part 2, Chemical and Microbiological Properties*. American Society of Agronomy, Madison, pp. 643–698.
- Killham, K., 1995. *Soil Ecology*. Cambridge University Press, Cambridge.
- Knops, J.M.H., Bradley, K.L., Wedin, D.A., 2002. Mechanisms of plant species impacts on ecosystem nitrogen cycling. *Ecology Letters* 5, 454–466.
- Llorens, E.M., 1995. Viewpoint: the state and transition model applied to the herbaceous layer of Argentina's Calden forest. *Journal of Range Management* 48, 442–447.
- Moretto, A.S., Distel, R.A., 1997. Competitive interactions between palatable and unpalatable grasses native to temperate semiarid grassland of Argentina. *Plant Ecology* 130, 155–161.
- Moretto, A.S., Distel, R.A., 2003. Decomposition of and nutrient dynamics in leaf litter and roots of *Poa ligularis* and *Stipa gnerioides*. *Journal of Arid Environments* 55, 503–514.
- Moretto, A.S., Distel, R.A., Didoné, N.G., 2001. Decomposition and nutrient dynamic of leaf litter and roots from palatable and unpalatable grasses in semiarid grassland. *Applied Soil Ecology* 18, 31–37.
- Pastor, J., Aber, J.D., Mc Clougherty, C.A., Melillo, J.M., 1984. Aboveground production and N and P cycling along a nitrogen mineralization gradient on Blackhawk Island, Wisconsin. *Ecology* 65, 256–268.
- Pisani, J.M., Distel, R.A., Bonatti, E.E., 2000. Diet selection by goats on a semiarid shrubland in central Argentina. *Ecología Austral* 10, 103–108.
- Rúgolo de Agrasar, Z.E., Steibel, P.E., Troiani, H.O., 2005. *Manual Ilustrado de las Gramíneas de la Provincia de La Pampa*. Universidad Nacional de La Pampa, Santa Rosa.
- Sall, J., Lehman, A., Creighton, L., 2001. *JMP® Start Statistics. A Guide to Statistics and Data Analysis Using JMP® and JMP IN® Software*, second ed. Duxbury–Thomson Learning, Pacific Grove.
- Semmartin, M., Aguiar, R.M., Distel, R.A., Moretto, A.S., Ghersa, C.M., 2004. Litter quality and nutrient cycling affected by grazing-induced species replacements along a precipitation gradient. *Oikos* 107, 148–160.
- Urquiaga, S., Cadisch, G., Alves, B.J.R., Boddey, R.M., Giller, K.E., 1998. Influence of decomposition of roots of tropical forage species on the availability of soil nitrogen. *Soil Biology and Biochemistry* 30, 2099–2106.
- Vitousek, P., 1982. Nutrient cycling and nutrient use efficiency. *American Naturalist* 119, 553–572.
- Wedin, D.A., 1995. Species, nitrogen, and grassland dynamics: the constraints of stuff. In: Jones, C.G., Lawton, J.H. (Eds.), *Linking Species and Ecosystems*. Chapman & Hall, New York, pp. 253–262.
- Wedin, D.A., 1999. Nitrogen availability, plant–soil feedbacks and grassland stability. In: Eldridge, D., Freudenberger, D. (Eds.), *People and Rangelands Building the Future. Proceedings of the VI International Rangeland Congress*, Townsville, pp. 193–197.
- Wedin, D.A., Tilman, D., 1990. Species effects on nitrogen cycling: a test with perennial grasses. *Oecologia* 84, 433–441.
- Wedin, D.A., Pastor, J., 1993. Nitrogen mineralization dynamics in grass monocultures. *Oecologia* 96, 186–192.