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Nutrient resorption from senescing leaves in two *Stipa* species native to central Argentina

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Abstract Nutrient resorption from senescing leaves enables plants to conserve and reuse nutrients. As such, it could be expected that plant species adapted to infertile soils have a higher nutrient resorption efficiency (percentage reduction of nutrients between green and senesced leaves) and/or higher nutrient resorption proficiency (absolute reduction of nutrients in senesced leaves) than those adapted to fertile soils. Our objective was to compare nitrogen (N) and phosphorous (P) resorption of two congener grasses that successfully occupy uplands of relatively low fertility (*Stipa gynerioides*) or lowlands of relatively high fertility (*Stipa brachychaeta*) in natural grasslands of central Argentina. The two *Stipa* species did not differ in N and P resorption efficiency, but *S. gynerioides* had a higher N and P resorption proficiency than *S. brachychaeta*. As a consequence, leaf-level N and P use efficiency were higher in the species adapted to low fertility conditions than in the species adapted to high fertility conditions. The higher nutrient resorption proficiency of *S. gynerioides* was also associated with relatively low leaf-litter decomposition and nutrient release rates found in a previous study.

Key words: nitrogen, nutrient resorption efficiency, nutrient resorption proficiency, nutrient use efficiency, phosphorous, *Stipa brachychaeta*, *Stipa gynerioides*.

INTRODUCTION

Nutrients may be mobilized from senescing leaves and transported to other plant tissues (nutrient resorption, *sensu* Killingbeck 1986), enabling plants to conserve and reuse them. As most of the nutrient capital of plants is contained in the leaves (Chapin 1980), nutrient resorption represents an important nutrient conservation mechanism. As such, it could be expected that plants adapted to infertile conditions should have a higher percentage reduction in the concentration of a nutrient between green and senesced leaves (nutrient resorption efficiency) and/or a lower nutrient concentration in senesced leaves (nutrient resorption proficiency) than those adapted to fertile conditions. Evidence shows no consistent genotypic differences in resorption efficiency in response to nutrient availability, but species from infertile environments tend to be more proficient at resorbing nutrients than those from fertile environments (Aerts 1996; Killingbeck 1996; Aerts & Chapin 2000). Killingbeck (1996) argued that the absolute level to which nutrients are reduced in senescing leaves (resorption proficiency) appears to be a more definitive and objective measure to estimate the degree to which selection has acted to minimize nutrient loss.

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The native grasslands located in the central part of Argentina are characterized by the abundance of grass species from the genus *Stipa* (Cabrera 1976). The distribution of *Stipa gynerioides* is restricted to nutrient-poor upland communities, whereas the distribution of *Stipa brachychaeta* is restricted to nutrient-rich lowland communities (Llorens 1995; Distel & Bóo 1996). In the present study we intended to address the question of whether these two congeners, adapted to different fertility conditions, differ in their nutrient resorption efficiency and proficiency. Considering the above background information, it could be expected that there would be similar resorption efficiencies in both *Stipa* species, but a higher resorption proficiency in *S. gynerioides*. Our objective was to determine the concentration of nitrogen (N) and phosphorus (P) in green and senesced leaves of *S. gynerioides* and *S. brachychaeta* for interspecific comparisons in nutrient resorption efficiency and proficiency. Because the *Stipa* species that inhabit central Argentina present peaks of growing activity in mid-autumn and mid-spring and dormancy in winter (Distel & Peláez 1985), interspecific comparisons were carried out at times of leave senescence in early winter and late spring. Due to the tight relationship between nutrient resorption proficiency and leaf-level nutrient use efficiency (Aerts 1990), species were also compared in N and P use efficiency. Nitrogen and P were selected because these nutrients represent the main growth-limiting nutrients for plants in natural environments (Chapin 1980). The comparison involved in the present study is particular as compares species of the same growth form and with similar phenology, sampled at the same time of the annual growing cycle and inhabiting contiguous sites differing in soil fertility.

METHODS

Samples were collected in the Caldén District (Cabrera 1976), on a site located in the south-eastern zone of La Pampa province in central Argentina (38°45′ S, 63°45′ W). The general characteristics of this region concerning climate, soil and vegetation have been described previously (INTA 1980). The climate of the region 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. More severe droughts occur during summer. Precipitation during the year of sampling was 560 mm. Dominant soils are distributed on uplands with interspersed lowlands (shallow depressions). Upland soils are coarse-textured Calciustolls of relatively low fertility, whereas lowland soils are fine-textured Haplustolls of relatively high fertility. Table 1 contains data on soil chemical properties in upland and lowland locations. Core soil samples ($n = 10$) for analysis were taken at 0–10 cm depth from upland and lowland locations in autumn. Soil organic matter was estimated from total organic carbon determined by dry combustion (Nelson & Sommers 1982) with an elemental analyser (Leco, model CR-1), total N by the semimicro Kjeldahl technique (Bremner & Mulvaney 1982), and plant-available P according to Bray and Kurtz (1945). The potential physiognomy of the vegetation was grassland with isolated woody plants (Distel & Bóo 1996). Late-seral dominant herbaceous species are represented by *Poa ligularis* in uplands and *Stipa clarazii* in lowlands. At present, after 100 years of heavy grazing by sheep and cattle on both landscape units, uplands are frequently dominated by *S. gynerioides* whereas lowlands are frequently dominated by *S. brachychaeta*. Both species are C3 cool-season bunchgrasses (Distel & Peláez 1985) of low preference for domestic livestock (Bóo *et al.* 1993; Pisani *et al.* 2000).

Table 1. Soil chemical properties in upland and lowland locations

Soil property	Upland	Lowland
Organic matter (%)	2.8 ± 0.1[a]	3.2 ± 0.1[b]
Total nitrogen (%)	0.120 ± 0.005[a]	0.174 ± 0.005[b]
Available phosphorous (p.p.m)	7.1 ± 0.6[a]	38.5 ± 3.5[b]

Values are mean ± SE ($n = 10$). [a,b]Different letters in a row indicate a significant difference ($P < 0.05$) after *t*-test analysis.

The sampling site was an area of 2 ha, fenced to exclude cattle grazing in the winter of 1998. Due to the rapid accumulation of dead biomass, the site was burned in February 1999. Plant samples were collected in June (winter) and November (spring) 1999, when the two *Stipa* species were in vegetative and reproductive stages of maturity, respectively. On each sampling occasion, 10 plants of *S. gynerioides* from upland locations and 10 plants of *S. brachychaeta* from lowland locations were harvested and transported to the lab. Fully expanded totally green and recently senesced leaves were sorted, dried at 60°C for 48 h and milled to pass through 1 mm mesh. Leaves were judged to be senescent when they were completely yellow without signs of deterioration. Senescence was more difficult to determine at the time of the winter sampling, which may have lead to the inclusion of some incompletely senesced leaves during the process of leaf sorting. Green and senesced leaves were analysed by the semimicro Kjeldahl method (for N) and the plasma emission spectrometry technique (for P; Benton Jones *et al.* 1991). Nitrogen and P concentrations in green and senesced leaves were used to calculate nutrient resorption efficiencies (Killingbeck 1996) and nutrient use efficiencies (Vitousek 1982) as follows:

$$\text{Nutrient resorption efficiency (\%)} = ((N_g - N_s)/N_g) \times 100$$

$$\text{Nutrient use efficiency (g dry matter/mg nutrient)} = 1/N_g \times (1 - r)$$

in which N_g is the nutrient concentration in green fully mature leaves, N_s is the nutrient concentration in senesced leaves and r is the nutrient resorption efficiency expressed as a fraction. Nutrient concentration in senesced leaves is considered a direct indicator of nutrient resorption proficiency (Killingbeck 1996). Changes in leaf mass associated with retranslocation during senescence can mask net changes in nutrient pools within tissues, creating a potential problem with nutrient resorption efficiency and proficiency values generated from measures of concentration changes. However, plants with more structural material show the lowest changes in leaf weight during senescence (Chapin 1980), and both *Stipa* species are high in structural material (Distel *et al.* 2000).

The data were analysed by a two-way ANOVA (two species by two seasons). Tukey–Kramer tests were carried out to determine the statistical significance of the differences between species/season combinations when the interaction species × season was significant ($P < 0.05$).

RESULTS

The concentrations of N and P in both green (Fig. 1) and senesced (Fig. 2) leaves were affected by species and season ($P < 0.01$). They were higher in *S. brachychaeta* than in *S. gynerioides* and higher in winter than in spring. The interaction between species and season was not significant for green leaves ($P > 0.05$), but was significant for N in senesced leaves ($P < 0.01$). The concentration of N in senesced leaves was higher in *S. brachychaeta* ($P < 0.05$) than in *S. gynerioides* in winter and spring. For *S. brachychaeta*, the concentration of N in senesced leaves was higher ($P < 0.05$) in winter than in spring, whereas for *S. gynerioides* it was similar ($P > 0.05$) in both seasons.

Nitrogen and P resorption efficiencies were influenced by season only ($P < 0.05$), being higher in spring than in winter (Fig. 3). The interaction between factors was significant for N only ($P < 0.01$). Nitrogen resorption efficiency was higher in *S. gynerioides* ($P < 0.05$) than in *S. brachychaeta* in winter only. For *S. brachychaeta*, N resorption efficiency was lower in winter than in spring ($P < 0.05$), whereas for *S. gynerioides* it was similar in both seasons ($P > 0.05$).

Nitrogen and P use efficiency varied with species and season ($P < 0.01$; Fig. 4). It was higher in *S. gynerioides* than in *S. brachychaeta* and higher in spring than in winter. The interaction between species and season was significant for both nutrients ($P < 0.01$). Nitrogen use efficiency was higher in *S. gynerioides* ($P < 0.05$) than in *S. brachychaeta* in winter and spring. For *S. brachychaeta*, N use efficiency was lower in winter than in spring ($P < 0.05$), whereas for *S. gynerioides* it was similar in both seasons ($P > 0.05$). Phosphorus use efficiency was higher in *S. gynerioides* than in *S. brachychaeta* in spring only ($P < 0.05$). For *S. gynerioides*, it was lower in winter than in spring ($P < 0.05$), whereas for *S. brachychaeta* it was similar in both seasons ($P > 0.05$).

DISCUSSION

Although the two *Stipa* species did not differ in the percentage reduction of N and P between green and senesced leaves (resorption efficiency; Fig. 3), they did differ in the absolute levels to which nutrients were reduced in senesced leaves (resorption proficiency; Fig. 2). As predicted, the species that occupied uplands of relatively low fertility (*S. gynerioides*) had higher nutrient resorption proficiencies than the species that occupied lowlands of relatively high fertility (*S. brachychaeta*). Plant species are considered

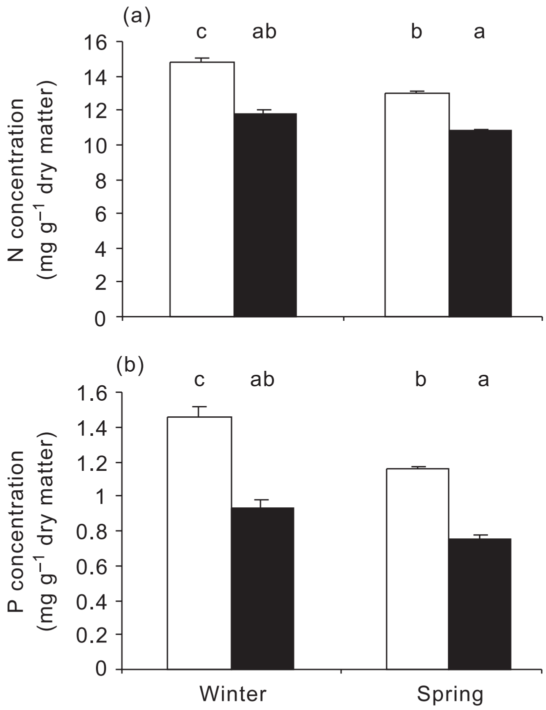

Fig. 1. (a) Nitrogen and (b) phosphorous concentration in green leaves by species and season. Mean ± SE ($n = 10$). Species and season effects are significant ($P < 0.01$). There was no species-by-season interaction ($P > 0.05$). (□), *Stipa brachychaeta*; (■), *Stipa gynerioides*. Different lower-case letters above columns indicate significant differences ($P < 0.05$).

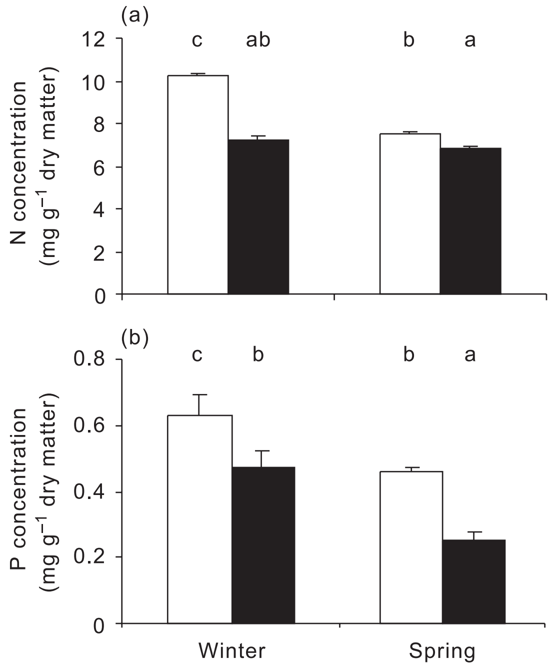

Fig. 2. (a) Nitrogen and (b) phosphorous concentration in senesced leaves by species and season. Mean ± SE ($n = 10$). Species and season effects are significant ($P < 0.01$). There was a species-by-season interaction ($P < 0.01$) for nitrogen only. Different lower-case letters above columns indicate significant differences ($P < 0.05$). (□), *Stipa brachychaeta*; (■), *Stipa gynerioides*.

highly proficient in nutrient resorption when they are able to reduce N and P in their senesced leaves to concentrations below 7 mg g^{-1} and 0.5 mg g^{-1}, respectively (Killingbeck 1996). The average N and P concentrations in senesced leaves of *S. gynerioides* (7.0 mg g^{-1} and 0.4 mg g^{-1}, respectively) and *S. brachychaeta* (8.9 mg g^{-1} and 0.5 mg g^{-1}, respectively) were close to these reference values. Nitrogen concentrations in senesced leaves of both *Stipa* species were similar to that reported for other graminoid species (8 mg g^{-1}), whereas P concentrations in senesced leaves of both *Stipa* species were lower than that reported for other graminoid species (1.0 mg g^{-1}; Jonasson & Chapin 1985; Berendse *et al.* 1987; Aerts & Berendse 1989). The relatively low concentrations of P in senesced leaves of *S. gynerioides* (0.25 mg g^{-1} in spring) is particularly important because of the low concentration of available P in upland soils (Table 1). Moreover, our results showed that N and P concentrations in senesced leaves can be subjected to significant temporal variability (Fig. 2). For example, P concentrations in senesced leaves were 37 and 88% higher in winter than in spring for *S. brachychaeta* and *S. gynerioides*, respectively. However, it is possible that at least some of this temporal variability in nutrient concentration in senesced leaves was due to incomplete senescence at the time of the winter sampling. In contrast, no significant intraspecific seasonal differences (winter *vs* spring) in the N concentrations of senesced leaves were found for three grasses inhabiting the Patagonian Monte in Argentina (*Stipa tenuis*, *Stipa speciosa* and *P. ligularis*; Carrera *et al.* 2000). More observation of temporal variability in nutrient concentrations in senesced leaves is needed in order to validate interspecific comparisons in nutrient resorption proficiency.

The similarities in nutrient resorption efficiency between the two congener species (Fig. 3) suggest that this parameter apparently does not explain their distribution over habitats differing in soil fertility. Lower seasonal variation in the concentration of N and P in green leaves (Fig. 1) than in senesced leaves (Fig. 2) resulted in higher nutrient resorption efficiencies in spring than in winter in both species, except for N resorption efficiency in *S. gynerioides*. This seasonal trend in nutrient resorption efficiency was opposite to the trend observed for three grasses in the Patagonian Monte, where seasonal variation in the concentration of N in green leaves was much larger than the corresponding variation in senesced leaves (Carrera *et al.* 2000). Temporal variability in nutrient resorption efficiency is common and poses a fundamental problem for interspecific comparisons (Killingbeck 1996). Average values of N resorption efficiency (37.8%) and

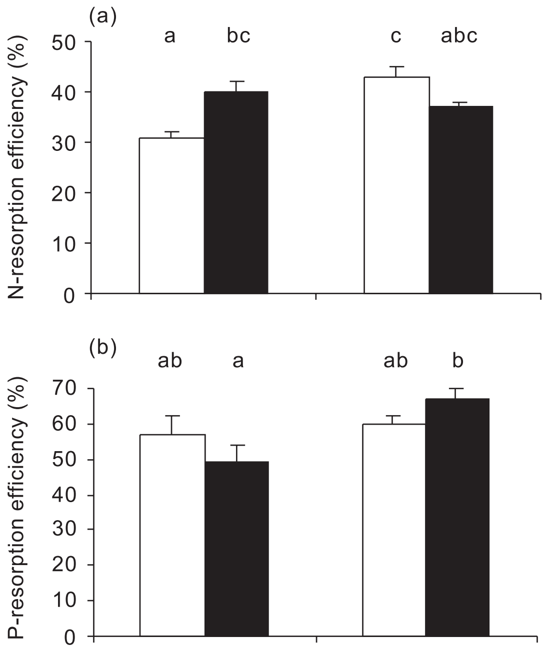

Fig. 3. Leaf-level (a) nitrogen and (b) phosphorous resorption efficiency by species and season. Mean ± SE ($n = 10$). Species effects are not significant ($P > 0.05$), whereas season effects are significant ($P < 0.05$). There was a species-by-season interaction ($P < 0.01$) for nitrogen only. Different lower-case letters above columns indicate significant differences ($P < 0.05$). (□), *Stipa brachychaeta*; (■), *Stipa gynerioides*.

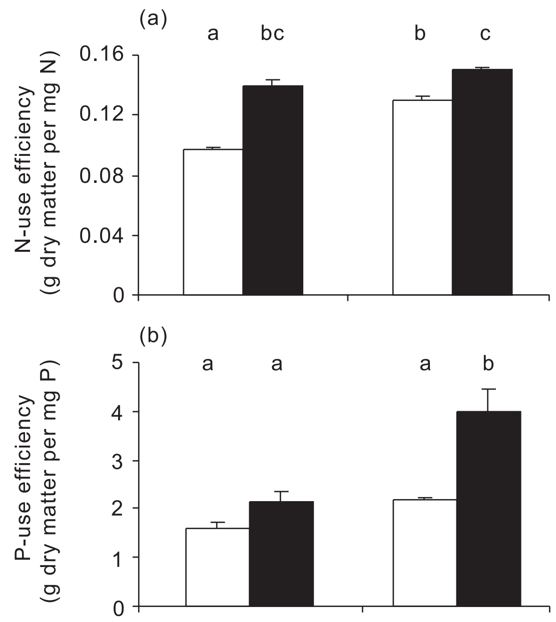

Fig. 4. Leaf-level (a) nitrogen and (b) phosphorous use efficiency by species and season. Mean ± SE ($n = 10$). Species and season effects are significant ($P < 0.01$). There was a species-by-season interaction ($P < 0.01$). Different lower-case letters above columns indicate significant differences ($P < 0.05$). (□), *Stipa brachychaeta*; (■), *Stipa gynerioides*.

P resorption efficiency (58.3%) were below the average values reported by Aerts (1996; 58.5 and 71.5%, respectively) and Killingbeck *et al.* (2002; 49.0 and 69.0%, respectively) for other graminoid species. Compared to perennial grasses analysed by Aerts (1996), on average, *S. gynerioides* and *S. brachychaeta* had lower concentrations of N in green leaves (12.6 *vs* 16.0 mg g^{-1}), similar concentrations of N in senesced leaves (7.9 *vs* 6.6 mg g^{-1}), similar concentrations of P in green leaves (1.1 *vs* 1.0 mg g^{-1}) and higher concentrations of P in senesced leaves (0.5 *vs* 0.3 mg g^{-1}). The average resorption efficiency for P was higher than that for N, being in agreement with analyses of large data sets involving different growth forms (Aerts & Chapin 2000).

The difference between the two *Stipa* species in nutrient resorption proficiency translated into interspecific differences in leaf-level nutrient use efficiency. Leaf mass produced per unit N or P taken up was higher in *S. gynerioides* than in *S. brachychaeta* (Fig. 4). However, a high leaf-level nutrient use efficiency does not necessarily correspond with a high whole-plant level NUE (Aerts 1990). The average value of N use efficiency of the *Stipa* species (0.13 g mg^{-1}) was slightly lower than that reported by Aerts (1996) for perennial grasses in the northern hemisphere (0.15 g mg^{-1}). On the contrary, the average value of P use efficiency of the two *Stipa* species (2.5 g mg^{-1}) was considerably lower than that reported by Aerts (1996; 3.7 g mg^{-1}). This discrepancy in P use efficiency can be explained by the higher average concentration of P in senesced leaves in the *Stipa* species. Also, the high nutrient proficiency of *S. gynerioides* is associated with relatively low leaf-litter decomposition and nutrient release rates (Moretto & Distel 2003). The existence of a positive feedback mechanism between low soil fertility and plant species adapted to such conditions has been highlighted by several authors (Berendse 1994; Jones *et al.* 1994; Aerts 1995; Wedin 1995). A positive feedback may contribute toward the high degree of persistence of *S. gynerioides* on uplands once it attains a high level of dominance, even if all grazing is removed (Distel & Bóo 1996).

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