SOIL RESOURCE ACQUISITION MECHANISMS, NUTRIENT CONCENTRATIONS AND GROWTH IN PERENNIAL GRASSES

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Species historically heavily grazed may have been selected for grazing-resistance traits associated with improved nutrient use efficiency (Chapin and Slack, 1979). Higher root length density (RLD) and vesicular-arbuscular mycorrhizae (VAM) colonization have been associated with greater nutrient acquisition in perennial grasses, thus contributing to competitive ability (Jackson and Caldwell, 1996). This is especially true in unproductive environments where competition for belowground resources is strong (Jackson and Caldwell, 1996). Mycorrhizal fungi can affect competitive interactions among plants hy improving soil nutrient uptake (Marschner and Dell, 1994; Mohammad *et al.*, 1998). However, lack of or even negative responses have been obtained under increased levels of mycorrhizal coloaization (Fitter and Hay, 1983).

Belowground competition is the major form of competition in semiarid and arid environments (Fowler, 1986). Occupation of soil space, which is of primary importance in belowground competition, depends on root characters such as length, which is of primary importance to acquire nutrients (Casper and Jackson, 1997). Species with less root length per soil volume, however, may be more dependent on mycorrhizal colonization for P acquisition than species with greater root length densities (Koide and Li, 1991). Greater root length densities and association with mycorrhizal-forming fungi can contribute to plant nutrient increase. However, these are often alternative strategies for nutrient acquisition by plants (Kothari *et al.*, 1990). Determination of the relative contribution of these mechanisms to plant competitive ability constitutes an iateresting and difficult research challenge (Derner and Briske, 1999). Studies of correlations among RLD, VAM colonization, plant biomass, soil P concentration, and concentration of P and N in plant tissues increase our understanding of the integration of plant shoot and root functions (Hetrick *et al.*, 1989).

The role of graziag by domestic livestock must be considered when evaluating strategies that contribute to competitive ability of rangeland vegetation. Factors that reduce photosynthetic capacity will also reduce soil resource acquisition mechanisms because these are dependent upon plant C fixation (Briske and Richards, 1995). Some grazing tolerant, competitive grass species (like *Agropyron desertorum*; Briske and Richards, 1995) are able to preferentially allocate C to regrowing shoot sinks while curtailing root growth after defoliation which allows for

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rapid photosynthetic canopy reestablishment. In contrast, root growth has remained unabated after defoliation in other grazing seositive, less competitive grasses (like *Pseudoroegneria spicata* Syn. *A. spicatum*; Briske and Richards, 1995) thus delaying reestablishment of a shoot/root equilibrium. Fungal simbiont biomass was doubled in *A. spicatum* and reduced by 50% in *A. deserıorum* after severe defoliation (Allen *et al.*, 1989). However, Allsopp (1998) suggested that any defoliation treatment would reduce percentage VAM colonization and external fungal hyphae in grass species with low competitive ability.

Root length density (RLD) and percent VAM colonization were evaluated in this study for *Stipa clarazii, S. tenuis* y *S. ambigua* after plants of these species were defoliated or remained undefoliated. These perennial tussock grasses have showo a different response to contiouous, long-term graziog in rangelands of central Argentina (Fernández and Busso, 1999). *S. clarazii* is palatable and dominant under exclosure or light grazing conditions (Cano, 1988; Busso, 1997). Fernández and Distel (1999) suggested that *S. clarazii* may have been ooe of the most abundant species in the herbaceous layer of the pristine vegetation in rangelands of central Argentina. This suggests that *S. clarazii* is a late-seral species (Saint Pierre *eı al.*, 2004). Because of selective herbivory, however, this species is replaced by *S. tenuis*, another palatable grass, under continuous, moderate grazing (Busso, 1997). At sites where grazing has been continuous and severe, however, *S. clarazii* and *S. tenuis* have been replaced by undesirable perennial grasses like *S. ambigua*, of earlier successional stages (Giorgetti *et al.*, 1997), which are grazed only when a better forage is not available (Cann, 1988). *S. clarazii* has shown a greater competitive ability and grazing tolerance than *S. tenuis* and *S. ambigua* when root proliferation and dry matter production of these species were determined in plants growing in isolation or in various neighborhoods exposed to different defoliation patterns (Saint Pierre *et al.*, 2000a, 2002; Saint Pierre, 2002). Io these studies, a neighborhood consisted of a central plant of one species surrounded by five neighboring plants of a different species. However, mechanisms contributing to its greater competitive ability are largely unexplored.

Our objectives were to examine: i) the effect of defoliation on shoot dry weight production and root traits and ii) the relationships between shoot and root characteristics. Since defoliation can diminish RLD and % VAM colonization by compromising carbohydrate supply to the fungi as an energy source, we hypothesized lower values for these parameters for defoliated than for intact control plants. We also hypothesized greater values for RLD and % VAM colonization on defoliated and undefoliated plants of *S. clarazii* than on those of the other two species, because of its greater competitive ability and defoliation tolerance.

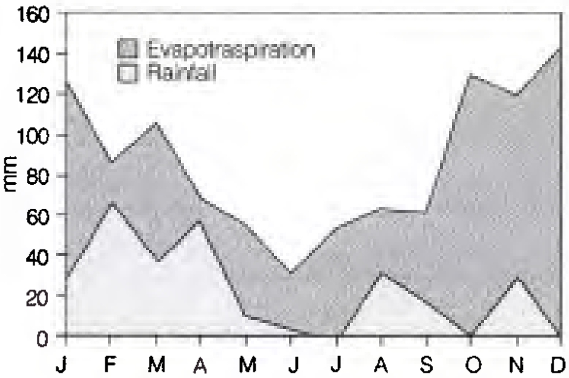

Figure 1. Mean monthly evapotranspiration and monthly rainfall during 1998 at a meteorological station located at the study site.

Materials and Methods

Study site

The study was conducted within a 2-year exclosure to domestic herbivory during 1998 at the *Chacra Experimental de Patagones*, south of the *Provincia de Buenos Aires* (40°39'S, 62°54'W), in the Phytogeographical Province of *El Monte* (Fernández and Busso, 1999). The community is characterized by an open shrubby layer, which also includes herbaceous species of different desirability for livestock production (Femández and Busso, 1999). Dominance of a particular grass species within the herbaceous layer at any site is determined, at least in part, by the previous grazing and fire history of that site (Fernández and Busso, 1999). The tree layer may be composed of occasional individuals of *Prosopis caldenia* Burkart. The soil was classified as a typical haplocalcid with an A horizon having a loamy-clay-sandy texture; 0.20m deep; 16.9g·kg^{-1} organic C; 28.7ppm available P and 1.23g·kg^{-1} total N. A B_w horizon was found below 0.20m of soil depth followed by a BC_k horizon between 0.28 and 0.43m of depth. A C_k horizon existed below 0.43m with very scarce roots. Average pH was 7. Long-term (1901-1950) mean annual values for rainfall were 331mm; 14.6°C fnr air temperature; -7.6°C (Aug) and 43°C (Jan) for absolute minimum and maximum air temperatures, respectively; 60% for relative humidity and 13km·h^{-1} for wind speed. Rainfall was 295.6mm in 1998. A meteorological statioo located at the *Chacra Experimental de Patagones* provided evapotranspiration and rainfall data during the study period (May to December, 1998; Figure 1).

Treatments and measurements on plants

A total of 72 plants of *S. clarazii, S. tenuis* and *S. ambigua* which had no neighbors within a radius of more than 0.5m were randomly selected. Plant circumference was measured at soil surface. Half of the plants were defoliated to 5cm stubble height on Sept 17 (apical meristems were not removed from the plants) and Oct 12 (apical meristems at the reproductive stage of development were removed), while the other half remained undefoliated (controls). Shoot dry weight production was measured at the time of the defoliation treatments (C, clipping). At the end of the growing cycle, the amount of dry weight produced by undefoliated control plants during the whole study period, and that produced by defoliated plants from the time of treatment to the end of the growing cycle (R, regrowth) were measured. Total dry weight produced by defoliated plants was calculated as C+R. All plant tissues obtained above clipping height were oven-dried at 60°C and then weighed. Current-year live and recently dead material were separated from older, previous-year tissues which had a grey color, weighed and ground to pass a 40-mesh screen. This separation based on leaf color was clear and reliable and it has been reported in several studies on perennial grasses (Busso *et al.*, 2001). Shoot P and N concentrations were determined following Chapman and Pratt (1961) and Nelson and Sommers (1980), respectively.

Three destructive harvests were conducted during spring on the following dates: 6-10 days after the first defoliation (Sept 26), 6-10 days after the second defoliation (Oct 22), and at the end of the growing season (Dec 2). Plants of the first harvest had been defoliated once while those of the second and third harvests had been defoliated twice. Four plants were harvested per species and defoliation treatment on each sam-

TABLE I
MEAN* VALUES FOR THE DIFFERENT MEASUREMENTS MADE IN PLANTS OF *S. clarazii, S. tenuis* AND *S. ambigua* WHICH WERE DEFOLIATED OR REMAINED UNDEFOLIATED DURING THE 1998 GROWING SEASON

	26 Sept		22 Oct		2 Dec	
	Undefoliated	Defoliated	Undefoliated	Defoliated	Undefoliated	Defoliated
Total dry weight (g·cm^{-2})						
S. clarazii	0.15±0.03a	0.12±0.02a	0.12±0.03a	0.16±0.09ab	0.13±0.05ah	0.17±0.02a
S. tenuis	0.11±0.02a	0.06±0.01a	0.05±0.02a	0.05±0.01a	0.05±0.02a	0.06±0.02b
S. ambigua	0.54±0.14b	0.31±0.05b	0.37±0.03b	0.32±0.02h	0.27±0.08h	0.31±0.02c
Regrowth production (g·cm^{-2})						
S. clarazii		0.001 ±0.001a		0.009 ±0.004a		0.042 ±0.016a
S. tenuis		0.003 ±0.001a		0.002 ±0.001b		0.019 ±0.009a
S. ambigua		0.003 ±0.001a		0.001 ±0.001b		0.010 ±0.005a
Root length density (cm·cm^{-3})						
S. clarazii	1.82±0.30a	2.57±0.27a	2.47±0.86a	1.54±0.46a	3.21±1.24a	2.34±0.93a
S. tenuis	2.20±0.50a	3.68±0.68a	2.76±1.02a	2.71±0.43a	1.71±0.38a	1.90±0.65a
S. ambigua	2.16±0.31a	2.40±0.23a	2.61±0.79a	1.49±0.45a	3.76±1.06a	7.94±0.80b
% VAM colonization						
S. clarazii	73.7±1.2a	60.6±7.8a	61.2±5.8a	67.5±2.7a	80.6±5.8a	70.0±6.8a
S. tenuis	65.0±5.9a	66.8±6.3a	75.0±3.9a	80.0±2.8a	63.7±5.5a	72.5±7.5a
S. ambigua	73.7±6.5a	70.6±7.6a	60.6±3.5a	73.7±4.1a	78.1±4.7a	74.3±1.5a
% soil P						
S. clarazii	15.9±1.5a	24.3±2.4a	9.4±3.1a	33.6±2.7ab	17.5±2.3a	47.1±4.2a
S. tenuis	37.0±3.4b	42.3±2.5b	33.1±3.4b	40.4±7.9h	22.3±3.6a	46.2±6.8a
S. ambigua	30.9±10.4b	27.9±3.1a	40.6±7.2b	24.4±7.0a	35.1±4.6b	19.9±2.7b
% tissue P						
S. clarazii	0.13±0.01a	0.12±0.01a	0.13±0.01a	0.15±0.01a	0.11±0.02a	0.19±0.03a
S. tenuis	0.18±0.01h	0.20±0.01b	0.14±0.01a	0.17±0.01a	0.10±0.01a	0.13±0.01h
S. ambigua	0.08±0.01c	0.17±0.02b	0.08±0.01b	0.12±0.01a	0.07±0.01a	0.13±0.01ab
% tissue N						
S. clarazii	1.14±0.05a	1.60±0.08a	1.10±0.06a	1.12±0.14a	1.06±0.17a	1.44±0.17a
S. tenuis	1.64±0.07b	1.52±0.05ab	1.05±0.10a	1.62±0.03b	0.89±0.10a	1.20±0.12a
S. ambigua	0.71±0.06c	1.25±0.13b	0.88±0.16a	1.25±0.16ab	0.79±0.05a	1.42±0.06a

* ±1SE, n=4.
Means within the same column followed by different letters are significantly different ($p<0.05$).

pling date. After harvesting, two soil cores (0.08m diameter) were taken at the periphery of each plant up to 0.30m depth. Becker *et al.* (1997) found that root weight density of field-grown *S. tenuis* and *Piptochaetium napostaense*, another native perennial grass in central Argentina, was more than two times higher between 0-0.25m than at 0.25-0.50m of soil depth. One of the soil cores was used to determine available soil P (Olsen and Sommers, 1982). The roots in the other soil core were used for determinations of both root length and frequency of mycorrhizal colonization.

Roots were removed from soil cores by manual washing using a 60-mesh sieve. Thereafter, root length was estimated using Tennant's method (1975). Since soil core volume was known (1507.96cm^3), RLD (cm roots cm^{-3} soil) could be calculated.

For mycorrhizal assessment, roots were cleared and stained according to Phillips and Hayman (1970). Percentages of root intercepts (n=40 per root sample) containing hyphae, arbuscules and/or vesicules were determinet using a microscope (x100). Colonized root length density was calculated by multiplying percentage colonization by root length density (Allen *et al.*, 1989).

Statistical analyses

A completely randomized design was used in all cases. Data were analyzed using a three-way analysis of variance (3 species x 2 defoliation treatments x 3 dates). When a significant ($p<0.05$) interaction or main treatment effect was found, mean values were compared using Fisher's least significant difference (LSD) test. Treatment means were considered significantly different at $p<0.05$. Data for colonized root length density were arcsin square root transformed. Plant biomass [ln(x+2)] and root length density (square root) data were also transformed. The figures and tables show untransformed means.

Relationships between variables were examined using linear regression analysis. Significance of these relationships was accepted at $p<0.05$. Regression lines were compared using the procedure described by Neter *et al.* (1985). Within each species, regression lines for defoliated and undefoliated plants were first compared and the data pooled if they were not significantly different ($p>0.05$).

Results

Dry weight production

Plant basal area was highly variable within and among treatments for all species. Minimum and maximum values were 15.6 and 108.9cm^2 in *S. clarazii*, 17.9 and 147.1cm^2 in *S. tenuis*, and 30.2 and 357.2cm^2 in *S. ambigua*. Differences in plant basal area between any species pair were the result of inherent size variation among species. Because of this, all dry weight production data are reported on a per surface plant basal area basis. The initial biomass (g·cm^{-2}) at the first clipping was 0.131 ±0.028 (mean ±1SE) in *S. clarazii*, 0.045 ±0.005 in *S. tenuis* and 0.304 ±0.017 in *S. ambigua*. Total dry weight production was more than 78% greater ($p<0.05$) on defoliated and undefoliated plants of *S. ambigua* than on those of the other two species (Tables I and II). However, the amount of regrowth was greater ($p<0.05$)

TABLE II

RESULTS OF A THREE-WAY ANALYSIS OF VARIANCE EXAMINING THE EFFECTS OF PLANT SPECIES, DEFOLIATION TREATMENT AND HARVEST DATE ON VALUES OBTAINED IN PLANTS OF *S. clarazii, S. tenuis* AND *S. ambigua* WHICH WERE DEFOLIATED OR REMAINED UNDEFOLIATED DURING THE 1998 GROWING SEASON

		Mean sums of squares					
	df	Total dry weight	Root length density	% VAM colonization	% soil P	% tissue P	% tissue N
Species	2	0.08970***	0.5469	0.00593	909.5***	0.00983***	0.47580**
Defoliation treatments	1	0.00064	0.2044	0.00022	925.2**	0.02569***	2.19940**
Dates	2	0.00206*	0.4591	0.02040	16.3	0.00481*	0.20793*
Species x Defoliation treatments	2	0.00003	0.1227	0.02642	1666.3***	0.00379*	0.12008
Species x Dates	4	0.00219*	1.0943**	0.03733*	224.0	0.00451**	0.26200**
Defoliation treatments x Dates	2	0.00399**	0.4660	0.03340	146.5	0.00175	0.03865
Species x defoliation treatments x dates	4	0.00076	0.3460	0.00972	206.8	0.00212	0.17855*
Error	54	0.00064	0.1932	0.01423	100.8	0.00095	0.04798

*p<0.05, **p<0.01, ***p<0.001

in *S. clarazii* than in *S. tenuis* and *S. ambigua*, at the end of the growing season (Table I).

Total dry weight production by undefoliated plants of all three species was greater (p<0.05) for the first and second than the last sampling date (Table I). As a result, total dry weight production of all three species was greater (p<0.05) for defoliated than on undefoliated plants at the end of the study period (Table I).

Root length density and percentage VAM colonization

Root length density was greater (p<0.05) in *S. ambigua* than in *S. clarazii* and *S. tenuis* (p<0.05) by the end of the growing season (Table I). This parameter was similar (p>0.30) for defoliated and undefoliated plants of all three species (Table I).

Percentage VAM colonization was similar among defoliation treatments (p>0.90, Tables I and II). All three species showed similar (p>0.05) VAM colonization percentages, except at the second sampling date, when this variable was greater (p<0.05) in *S. tenuis* than in *S. clarazii* (Tables I and II). Values for this parameter varied from 61 to 81% in *S. clarazii, S. tenuis* and *S. ambigua* (Table I). Percentages of VAM colonization increased (p<0.05) from the second to the last sampling date in *S. clarazii*, and from the first to the second sampling in *S. tenuis* (Tables I and II).

Shoot P and N concentrations

Tissue P concentrations were more than 20% greater (p<0.05) on defoliated than on undefoliated plants in *S. clarazii* and *S. ambigua* (Table I). Tissue P concentrations of defoliated plants were similar (p>0.05) in *S. clarazii, S. tenuis* and *S. ambigua* (Table I). When plants remained undefoliated, however, tissue P concentrations were more than 38% lower (p<0.05) in *S. ambigua* than in *S. clarazii* and *S. tenuis* (Table I).

S. ambigua was the species that showed the lowest (p<0.05) tissue P concentrations in comparison to *S. tenuis, S. tenuis* and *S. clarazii*, or *S. clarazii* at the first, second or last sampling date, respectively (Tables I and II). Tissue P concentrations were similar (p<0.05) among sampling dates in *S clarazii* and *S. ambigua*, and they decreased (p<0.05) as the growing season progressed for *S. tenuis* (Tables I and II).

Nitrogen concentrations for plants of all three species defoliated twice were more than 31% greater (p<0.05) than values of undefoliated controls (Tables I and II).

Available soil P concentrations

Soil P concentrations increased (p<0.05) when plants of *S. clarazii* and *S. tenuis* were defoliated in comparison to undefoliated controls, and the reverse was true in *S. ambigua* (Tables I and II). When plants remained undefoliated, soil P concentrations were greater (p<0.05) under shoots of *S. tenuis* and *S. ambigua* than under those of *S. clarazii*. However, soil under defoliated *S. clarazii* and *S. tenuis* showed higher (p<0.05) P concentrations than that under defoliated *S. ambigua* (Tables I and II).

Relationships between shoot and root variables

Only data demonstrating significant correlations are reported. Lack of more consistent associations in this field study may partly be the result of the small sample size (n=4), which is the minimum for detecting correlations. Root length density was positively correlated (p<0.05, r=0.65, n=14) with total dry weight production on plants which remained undefoliated or were defoliated twice in *S. tenuis* (Figure 2a). RLD and percentage VAM colonization showed a negative correlation (p<0.05, r=0.72, n=8) in *S. clarazii* plants that were defoliated twice during the growing season (Figure 2b).

Plants of *S. tenuis* that remained undefoliated or were defoliated once showed a positive correlation (p=0.05, r=0.70, n=8) between RLD and tissue P concentration (Figure 2c). A similar response between these two variables (p<0.05, r=0.79, n=8) was obtained nn plants of *S. ambigua* that were defoliated once or twice in the study period (Figure 2d). Tissue N concentrations of *S. clarazii* plants that were defoliated twice (p<0.05, r=0.84, n=6; Figure 2e) and on those of *S. ambigua* that were defoliated once or twice (p<0.05, r=0.61, n=11; Figure 2f) were positively correlated with RLD.

Percentage VAM colonization and tissue P concentration were positively correlated (p<0.01, r=0.99, n=4) in *S. tenuis* after 6-10 days from the first defoliation (Figure 3a). These plants, however, showed a negative correlation (p=0.05, r=0.95, n=4) between percentage VAM colonization and total dry weight production (Figure 3b). This response was mostly the result of the negative correlation (p<0.05, r=0.91, n=6) between tissue P concentration and total dry weight production.

Available soil P was negatively correlated (p<0.01, r=0.84, n=8) with percentage VAM colonization on defoliated and undefoliated plants of *S. clarazii* at the first sampling date (Figure 4).

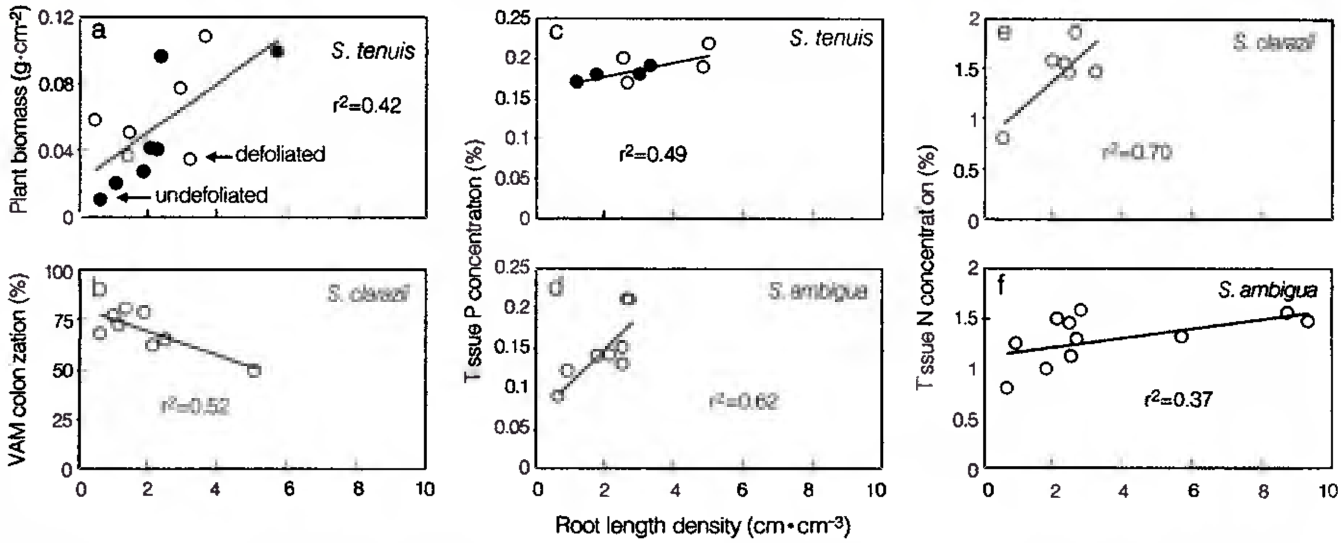

Figure 2. Relationship between root length density and a: total dry weight production of plants of *S. tenuis* which remained undefoliated or were defoliated twice during the growing season; b: percentage VAM colonization of defoliated plants of *S. clarazii*; c: tissue P concentration of plants of *S. tenuis* which remained undefoliated or were defoliated once during the growing season; d: tissue P concentration of defoliated plants of *S. ambigua*; e and f: tissue N concentration of plants of *S. clarazii* which were defoliated twice and of plants of *S. ambigua* which were defoliated once or twice, respectively. All relationships were significant at $p<0.05$.

Discussion

Since dry weight accumulated at the time of the first defoliation was more than 75% of total dry weight production of defoliated plants of the three species, initial biomass appeared to be the major determinant of that total dry weight production. Total dry weight did nnt increase and sometimes decreased with age during spring for undefoliated plants of the three species (Table I). Standing crop declines have been reported in other perennial grasses during the growing season, and have been attributed to translocation, leaching, oxidation, leaf dropping and seed dissemination (Turner and Klipple, 1952; Pieper, 1978).

Towards the end of the growing season, regrowth production was greater ($p<0.05$) in *S. clarazii* than in the other two species (Table I). In a parallel study on the same plants, *S. clarazii* showed more than 150% greater relative growth rates and more than 33% greater daughter tiller production than *S. tenuis* and *S. ambigua* (Saint Pierre *et al.*, 2000b). Because greater growth rates are positively related to competitive ability (Grime, 1979), our results suggest that *S. clarazii* is a superior competitor when compared to *S. tenuis* and *S. ambigua*. Rapid growth rates after defoliation also contribute to herbivory tolerance (Briske and Richards, 1995). Similar to the finding of Anderson and Briske (1995), nur study showed that late-seral species can have an either similar or greater herbivory tolerance than earlier-seral species. Selective defoliation of late-seral species, however, would be the dominant mechanism leading to their replacement by earlier-seral species in the community (Anderson and Briske, 1995).

Lack of significant differences in root length density between defoliated and undefoliated plants suggested that photosynthetic canopy reestablishment may be achieved without sacrificing RLD in all three species, at least as long as C reserves do not become limiting. An immediate root growth reduction after defoliation would allow preferential allocation of C resources to regrowing shoots, thus rapidly reestablishing a photosynthetic canopy and returning to a shoot/root equilibrium (Davidson, 1978; Briske and Richards, 1995). Root growth reductions after defoliation could then be an important determinant of tolerance to herbivory and competitive ability in grass species (Richards, 1984). In our study, RLD and total dry weight production were positively correlated for defnliated and undefoliated plants of *S. tenuis* (Figure 2a). Root length density also showed positive correlations with tissue N and P concentrations in *S. clarazii, S. tenuis* and *S. ambigua* (Figure 2c-f). Under local soil nutrient supply conditinns, it appeared that root activity must be maintained after defoliation in these species to reestahlish a green surface area rapidly and keep resource supply to the plant at equilibrium (Chapin and Slack, 1979). For example, high root densities allowed nutrient exploitation in *Schizachyrium scoparium* under very low soil nutrient concentrations (Wedin and Tilman, 1993). Past selection pressure on plants and the nature of grazing itself prohably contribute to the ability of grasslands to sustain or increase root biomass under defoliation (McNaughton *et al.*, 1998). In particular, it seems likely that a long evolutionary history of co-occurrence of forages and grazers has led to feedback mechanisms that diminish the immediate detrimental effects of defoliation on soil resource acquisition (Milchunas *et al.*, 1988).

Similar to the findings in previous studies (Allen *et al.*, 1989; Busso *et al.*, 2001), defoliation did not affect levels of VAM colonization in *S. clarazii, S. tenuis* or *S. ambigua*. Apparently, defoliation did not remove sufficient photosynthetic tissue to reduce substrate availability to fungi for sufficient periods to reduce infection rates (Trent *et al.*, 1988). Other workers, however, have reported either decreases or increases in percentage colonization by VAM after defoliation (Bethlenfalvay and Dakessian, 1984). This plasticity in the response of VAM to defoliation might be a major reason for their persistence and importance in native ecosystems (Allen *et al.*, 1989). Other factors such as water stress, timing of defoliation and species-specific physiological traits can also influence mycorrhizal symbiosis (Allen *et al.*, 1989), and may thus have affected nur observed plant responses.

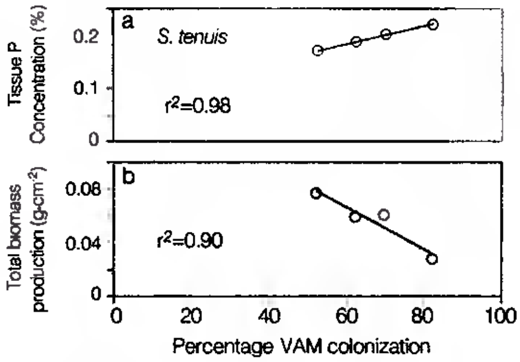

Figure 3. Relationship between percent VAM colonization and a: tissue P concentration or b: total dry weight production of plants of *S. tenuis* 6-10 days after the first defoliation. Both relationships were significant at $p \leq 0.05$.

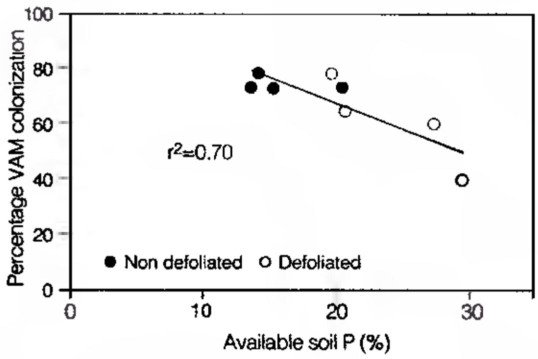

Figure 4. Relationship between available soil P and percentage VAM colonization of plants of *S. clarazii* which remained undefoliated or were defoliated once (6-10 days after the first defoliation) during the growing season. The relationship was significant at $p<0.01$.

Percentages of vesicular-arbuscular mycorrhizae in the three species were similar to values found for other C_3 and C_4 annual or perennial grasses (Busso *et al.*, 2001). However, our results contrast with studies which report that C_3 plants are only weakly dependent on mycorrhizal symbiosis even under low levels of available P in native prairie soils (Hetrick *et al.*, 1989). Diffusion rate of ions in the soil solution, rather than uptake kinetics, appears to be the limiting factor for nutrient absorption in nutrient-poor environments. This is because nutrient availability is low on average, and nutrients beyond depletion zones must diffuse towards the roots (Wedin and Tilman, 1993). Fungal hyphae can cross depletion zones and transport P to the roots for a much smaller biomass investment than roots (Fitter and Hay, 1983). Thus, species with high uptake kinetics face a disadvantage in these environments because their high C costs associated with construction and maintenance of absorption mechanisms do not translate into higher nutrient absorption (Aerts, 1999). Under these conditions, physiological mechanisms are likely to be less important than morphological mechanisms or those related to a greater exploration of the soil volume (Jackson and Caldwell, 1996). This may be one explanation for the high VAM colonization percentages in all three C_3 perennial grass species.

Shoot nutrient concentrations were greater for defoliated than undefoliated plants of all three species (Table I). It has been widely reported that concentrations of P and N are higher in younger than older plant tissues (Mengel and Kirkby, 1982). Undefoliated plants of the unpalatable *S. ambigua* showed the lowest P and N concentrations in comparison to *S. clarazii* and *S. tenuis* (Table I). Other studies have already reported lower nutrient concentrations in unpalatable than in palatable perennial grasses (Cano, 1988; Wedin, 1995). Poorer litter quality in the unpalatable grasses may reduce nutrient turnover and soil nutrient availability (Berendse, 1994; Wedin, 1995). In agreement with these findings, soil under defoliated *S. clarazii* and *S. tenuis* canopies had greater available P concentrations than under *S. ambigua* canopies (Table I). Greater nutrient uptake rates on undefoliated plants of *S. clarazii* than on those of *S. tenuis* and *S. ambigua* (Giorgetti *et al.*, 2000), however, may help explain the lower available soil P concentrations under *S. clarazii* than under *S. tenuis* and *S. ambigua* canopies when plants remained undefoliated.

Mycorrhizal dependency appears to be negatively related to root parameters such as root length and surface area at least for P uptake (Kothari *et al.*, 1990). The negative correlation between percentage VAM colonization and root length density on plants of *S. clarazii* defoliated twice (Figure 2b) could represent a mechanism that allows this species to reduce C loss to the fungal symbiont when nutrient supply to the plant is adequate. Total length of the root system was reduced on plants of *Schizachyrium scoparium* after it was colonized by VAM (Anderson and Liberta, 1992). Similarly, Kothari *et al.* (1990) found that the most profound effect of VA mycorrhizal fungi in *Zea mays* was on root growth and morphology; root dry weight decreased by 16%, root length by 31% and root hair density and length by 41 and 43%, respectively.

There was a negative correlation between percentage VAM colonization and the P content of soil for plants of *S. clarazii* which remained undefoliated or those that were defoliated once during the growing season (Figure 4). This result, which confirms other studies demonstrating that VAM colonization is reduced in soils of higher P availability (Mohammad *et al.*, 1998), suggests a strategy allowing *S. clarazii* to avoid shifts from mutualism to parasitism in the plant-mycorrhizae relationship. If soil P is not limiting, investment in a mycorrhizal association may not result in enhanced plant growth (Anderson and Liberta, 1992). However, several authors have reported that tissue P concentration of the host plant can also control VAM colonization levels (Tawaraya *et al.*, 1994). As a result, the inhibition mechanism of VAM colonization because of the P content in the plant-soil system has not yet been fully documented (Tawaraya *et al.*, 1996). It has even been suggested that depression of VAM colonization under high soil P contents is influenced by soil N availability (Marschner and Dell, 1994).

Except on plants of *S. tenuis* defoliated once, where percentage of VAM colonization and tissue P concentration showed a positive relationship (Figure 3a), percentages of VAM colonization did not correlate with shoot N or P concentrations in any other treatment. The negative correlation between tissue P concentration and total dry weight production in *S. tenuis* most likely reflected a dilution effect resulting from dry weight increases (Mengel and Kirkby, 1982). Experiments carried out in the field or under controlled environmental conditions have shown that mycorrhizal plants of several perennial grass species accumulated more P or N and/or had greater P or N concentrations than their non-mycorrhizal counterparts (Call and Davies, 1988; Hetrick *et al.*, 1993; Trent *et al.*, 1993; Noyd *et al.*, 1995). However, mycorrhizal and non-mycorrhizal plants of *Bromus inermis* had similar total P concentrations (Hetrick *et al.*, 1994).

Greater regrowth production in the more grazing tolerant and competitive species, *S. clarazii*, than in the less grazing tolerant and competitive *S. tenuis* and *S. ambigua* could not be explained by a greater RLD or percentage

VAM colonization in our study. These variables were similar on defoliated and undefoliated plants in all three species. Saint Pierre *et al.* (2002) reported that both greater root length and dry weight increases in *S. clarazii* after defoliation appear determinant in contributing to explain its greater competitive ability and defoliation tolerance when compared with the other two species.

REFERENCES

Aerts R (1999) Interspecific competition in natural plant communities: mechanisms, trade-offs and plant-soil feedback. *J. Exp. Bot. 50*: 29-37.

Allen MF, Richards JH, Busso CA (1989) Influence of clipping and soil water status on vesicular-arbuscular mycorrhizae of two semi-arid tussock grasses. *Biol. Fertil. Soils. 8*: 285-289.

Allsopp N (1998) Effect of defoliation on the arbuscular mycorrhizae of three perennial pasture and rangeland grasses. *Plant Soil 202*: 117-124.

Anderson RC, Liberta AE (1992) Influence of supplemental inorganic nutrients on growth, survivorship, and mycorrhizal relationships of *Schizachyrium scoparium* (Poaceae) grown in fumigated and unfumigated soil. *Amer. J. Bot. 79*: 406-414.

Anderson VJ, Briske DD (1995) Herbivore-induced species replacement in grasslands: is it driven by herbivory tolerance or avoidance? *Ecol. Appl. 5*: 1014-1024.

Becker GF, Busso CA, Montani T, Burgos MA, Flemmer AC, Toribio MB (1997) Effects of defoliating *Stipa tenuis* and *Piptochaetium napostaense* at different phenological stages. III. Root growth. *J. Arid Environ. 35*: 269-283.

Berendse F (1994) Litter decomposability - a neglected component of plant fitness. *J. Ecol. 82*: 187-190.

Bethlenfalvay GJ, Dakessian S (1984) Grazing effects on mycorrhizal colonization and floristic composition of the vegetation on a semiarid range in northern Nevada. *J. Range Manag. 37*: 312-316.

Briske DD, Richards JH (1995) Plant response to defoliation: A physiologic, morphologic and demographic evaluation. In Bedunah DJ, Sosebee RE (Eds.) *Wildland Plants: Physiological Ecology and Developmental Morphology*. Society for Range Management. Denver, Colorado, USA. pp. 635-710.

Busso CA (1997) Towards an increased and sustainable production in semiarid rangelands of Central Argentina: Two decades of research. *J. Arid. Environ. 36*: 197-210.

Busso CA, Briske DD, Olalde-Portugal V (2001) Root traits associated with nutrient exploitation following defoliation in three coexisting perennial grasses in a semi-arid savanna. *Oikos 92*: 332-342.

Call CA, Davies FT (1988) Effects of vesicular-arbuscular mycorrhizae on survival and growth of perennial grasses in lignite overburden in Texas. *Agr. Ecosyst. Environ. 24*: 395-405.

Cano E (1988) *Pastizales naturales de La Pampa. Descripción de las especies más importantes*. Tomo 1. Convenio AACREA-Provincia de La Pampa, Argentina. 425 pp.

Casper BB, Jackson RB (1997) Plant competition underground. *Ann. Rev. Ecol. Sys. 28*: 545-570.

Chapin FS III, Slack M (1979) Effect of defoliation upon root growth, phosphate absorption and respiration in nutrient-limited tundra graminoids. *Oecologia* (Berl.) *42*: 67-79.

Chapman HD, Pratt PF (1961) *Methods of analysis for soils, plants and waters*. University of California, Riverside, CA, USA. 309 pp.

Davidson RL (1978) Root systems the forgotten component of pastures. In Wiklson JR (Ed.) *Plant relations in pastures*. CSIRO. East Melbourne, Australia. pp. 86-94.

Derner JD, Briske DD (1999) Does a tradeoff exist between morphological root plasticity? A comparison of grass growth forms. *Acta Oecol. 20*: 519-526.

Fernández OA, Busso CA (1999) Arid and semi-arid rangelands: two thirds of Argentina. In Arnalds O, Archer S (Eds.) *Case Studies of Rangeland Desertification*. Agricultural Research Institute Report N° 200. Reykjavik, Iceland. pp 41-60.

Fernández OA, Distel RA (1999) Management guidelines for sustainable use in rangelands of central Argentina. *Proc. VI Int. Rangeland Cong.: People and Rangelands, Building the Future*. Townsville, Australia. pp. 1026-1027.

Fitter AH, Hay RKM (1983) *Environmental Physiology of Plants*. Academic Press. New York, USA. 355 pp.

Fowler NL (1986) The role of competition in plant communities in arid and semiarid regions. *Ann. Rev. Ecol. Sys. 17*: 89-110.

Giorgetti HD, Montenegro OA, Rodríguez GD, Busso CA, Montani T, Burgos MA, Flemmer AC, Toribio MB, Horvitz SS (1997) The comparative influence of past management and rainfall on range herbaceous standing crop in east central Argentina: 14 years of observations. *J. Arid Environ. 36*: 623-637.

Giorgetti HD, Saint Pierre C, Busso CA, Montenegro OA, Rodríguez GD, Montani T, Bravo OA (2000) Tasa de absorción de ^{15}N como medida de la capacidad competitiva de especies de gramíneas perennes. *XXIII Congresa Argentina de Producción Animal*. Corrientes, Argentina. pp. 137-138.

Grime JP (1979) *Plant Strategies and Vegetation Processes*. Wiley. New York, USA. 222 pp.

Hetrick BAD, Wilson GWT, Hartnett DC (1989) Relationship between mycorrhizal dependence and competitive ability of two tallgrass prairie grasses. *Can. J. Bot. 67*: 2608-2615.

Hetrick BAD, Hartnett DC, Wilson GWT, Gibson DJ (1993) Effects of mycorrhizae, phosphorus availability, and plant density on yield relationships among competing tallgrass prairie grasses. *Can. J. Bot. 72*: 168-176.

Hetrick BAD, Wilson GWT, Schwab AP (1994) Mycorrhizal activity in warm- and cool-season grasses: variation in nutrient-uptake strategies. *Can. J. Bot. 72*: 1002-1008.

Jackson RB, Caldwell MM (1996) Integrating resource heterogeneity and plant plasticity modelling nitrate and phosphate uptake in a patchy soil environment. *J. Ecol. 84*: 891-903.

Koide RT, Li M (1991) Mycorrhizal fungi and the nutrient ecology of three oldfield annual plant species. *Oecologia 85*: 403-412.

Kothari SK, Marschner H, George E (1990) Effect of VA mycorrhizal fungi and rhizosphere microorganisms on root and shoot morphology, growth and water relations in maize. *New Phytol. 116*: 303-311.

Marschner H, Dell B (1994) Nutrient uptake in mycorrhizal symbiosis. *Plant Soil 159*: 89-102.

McNaughton SJ, Banyikwa FF, McNaughton MM (1998) Root biomass and productivity in a grazing ecosystem: the Serengeti. *Ecology 79*: 587-592.

Mengel K, Kirkby EA (1982) *Principles of Plant Nutrition*. International Potash Institute. Worblaufen-Bern, Switzerland. 655 pp.

Milchunas DG, Sala OE, Lauenroth WK (1988) A generalized model of the effects of grazing by large herbivores on grassland community structure. *Am. Naturalist 132*: 87-106.

Mohammad MJ, Pan WL, Kennedy AC (1998) Seasonal mycorrhizal colonization of winter wheat and its effect on wheat growth under dryland field conditions. *Mycorrhiza 8*: 139-144.

Nelson DW, Sommers LE (1980) Total nitrogen analysis of soil and plant tissues. *J. Assoc. Off. Anal. Chem. 63*: 770-778.

Neter J, Wasserman W, Kutner MH (1985) *Applied linear statistical models: regression, analysis of variance, and experimental designs*. RD Irwin. Homewood, Illinois, USA. 1127 pp.

Noyd RK, Pfleger FL, Russelle MP (1995) Interactions between native prairie grasses and indigenous arbuscular mycorrhizal fungi: Implications for reclamation of taconite iron ore tailing. *New Phytol. 129*: 651-660.

Olsen SR, Sommers LE (1982). Phosphorus. In Page AL, Miller RH, Keeney DR (Eds.). *Methods of Soil Analysis*. Part. 2. American Society of Agronomy. Madison, USA. pp. 403-430.

Phillips JM, Hayman DS (1970) Improved procedures for clearing roots and staining parasitic and vesicular-arbuscular mycorrhizal fungi for rapid assessment of infection. *Trans. Br. Mycol Soc. 55*: 158-162.

Pieper RD (1978) *Measurement techniques for herbaceous and shrubby vegetation*. New Mexico State University. Las Cruces, New Mexico, USA. 148 pp.

Richards JH (1984) Root growth response to defoliation in two Agropyron bunchgrasses: field observations with an improved root periscope. *Oecologia (Berl) 64*: 21-25.

Ryser P, Lambers H (1995) Root and leaf attributes accounting for the performance of fast- and slow-growing grasses at different nutrient supply. *Plant Soil 170*: 251-265.

Saint Pierre C (2002) Capacidad competitiva y tolerancia a la defoliación en *Stipa clarazii, Stipa tenuis* y *Stipa ambigua*. Universidad Nacional del Sur. Bahía Blanca, Buenos Aires, Argentina. 81 pp.

Saint Pierre C, Busso CA, Montenegro OA, Rodríguez GD, Giorgetti HD, Montani T (2000a). Producción de materia seca en especies de gramíneas perennes nativas del centro de Argentina. *XVI Reunión Latinoamericana de Producción Animal, III Congreso Uruguayo de Producción Animal*. Montevideo, Uruguay.

Saint Pierre C, Busso CA, Montenegro OA, Rodríguez GD, Giorgetti HD, Montani T. (2000b) Demografía y crecimiento en espe-

cies de gramíneas nativas del Sur de la Provincia Fitogeográfica del Monte. *XVI Reunión Latinoamericana de Producción Animal, III Congreso Uruguayo de Producción Animal.* Montevideo, Uruguay.

Saint Pierre C, Bussn CA, Montenegro OA, Rndríguez GD, Giorgetti HD, Montani T, Bravo OA (2002) Root proliferation in perennial grasses of low and high palatahility. *Plant Ecol. 165*: 161-169.

Saint Pierre C, Busso CA, Montenegro OA, Rodríguez GD, Giorgetti HD, Mantani T, Bravo OA (2004) Direct assessment of competitive ability and defoliation tolerance in perennial grasses. *Can. J. Plant Sci. 84*: 195-204.

Tawaraya K, Saito M, Morinka M, Wagatsuma T (1994) Effect of phosphate application to arbuscular mycorrhizal onion on the development and succinate dehydrogenase activity of internal hyphae. *Soil Sci. Plant Nutr. 40*: 111-117.

Tawaraya K, Saito M, Morioka M, Wagatsuma T (1996) Effect of concentration of phosphate on spore germination and hyphal growth of arbuscular mycorrhizal fungus, *Gigaspora margarita* Becker & Hall. *Soil Sci. Plant Nutr. 42*: 667-671.

Tennant D (1975) A test of a modified line intersect method of estimating root length. *J. Ecol. 63*: 995-1001.

Trent JD, Wallace L, Svejcar TJ, Christiansen S (1988) Effect of grazing on growth, carbohydrate pools, and mycorrhizae in winter wheat. *Can. J. Plant Sci. 68*: 115-120.

Trent JD, Svejcar AJ, Bethlenfalvay GJ (1993) Growth and nutrition of comhinations of native and introduced plants and mycorrhizal fungi in a semiarid range. *Agr. Ecosyst. Environ. 45*: 13-23.

Turner GT, Klipple TE (1952) Growth characteristics of blue grama in northeastern Colorado. *J. Range Manag. 5*: 22-28.

Wedin DA (1995) Species, nitrogen, and grassland dynamics: the constraints of stuff. In Jones CG, Lawton JH (Eds.) *Linking species and Ecasystems*. Chapman and Hall. New York, USA. pp. 253-262.

Wedin D, Tilman D (1993) Competition amnng grasses along a nitrogen gradient: Initial conditions and mechanisms of competitinn. *Ecol. Monogr. 63*: 199-229.