

Direct assessment of competitive ability and defoliation tolerance in perennial grasses

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Saint Pierre, C., Busso, C. A., Montenegro, O. A., Rodriguez, G. D., Giorgetti, H. D., Montani, T. and Bravo, O. A. 2004. **Direct assessment of competitive ability and defoliation tolerance in perennial grasses.** Can. J. Plant Sci. **84**: 195–204. *Stipa clarazii* is a dominant, late-seral perennial grass species under enclosure or lightly grazed rangelands in semiarid Argentina, whereas *S. tenuis* and *S. ambigua* are earlier-seral perennial tussock grasses. Recent studies have demonstrated that late-seral species are more competitive and can have either similar or greater herbivory tolerance than earlier-seral species. We hypothesized that (1) tolerance to defoliation is greater on defoliated plants of *S. clarazii* than on those of *S. tenuis* and *S. ambigua*, (2) competitive ability is greater in *S. clarazii* than in *S. tenuis* and *S. ambigua* when plants remain undefoliated or are exposed to a comparable defoliation intensity, and (3) competitive ability decreases in *S. clarazii* when this species is selectively defoliated within a non-defoliated, nearby neighbourhood of *S. tenuis* or *S. ambigua*. The study objectives included obtaining a direct measure of competitive ability and defoliation tolerance in the three perennial grasses when they grew either in isolation or in different neighbourhoods and were exposed to various defoliation patterns in the field. In 1998, two parallel studies were conducted within a 2-yr-old field enclosure during one growing season. In one study, responses were evaluated on either defoliated or undefoliated plants of all three species without neighbours. In a second experiment, four types of neighborhoods were selected such that a central (target) plant of one species was surrounded by five neighboring plants of a different species. Three different defoliation patterns were imposed on each neighbourhood type. Results led to acceptance of the first and second and rejection of the third hypothesis. When plants grew without nearby neighbours, greater growth rates for height, dry matter production and end-of-season daughter tiller production per parent tiller in *S. clarazii* relative to *S. tenuis* and *S. ambigua* contributed to greater regrowth in *S. clarazii*. Amounts of ¹⁵N atom excess were always greater in *S. clarazii* than in *S. tenuis* and *S. ambigua* independently of neighbourhood type and pattern of defoliation. However, uptake of ¹⁵N was similar in *S. clarazii* to that in *S. tenuis* or *S. ambigua* when *S. clarazii* was selectively defoliated within a non-defoliated, nearby neighbourhood of any of the other two species. Selective herbivory of *S. clarazii*, rather than factors associated with its competitive ability and defoliation tolerance, were found to be the major determinant driving its replacement by earlier-seral, less desirable perennial grasses in rangelands of central Argentina.

Key words: ¹⁵N, Argentina rangelands, biomass, nitrogen uptake, species replacement, *Stipa*

Saint Pierre, C., Busso, C. A., Montenegro, O. A., Rodriguez, G. D., Giorgetti, H. D., Montani, T. et Bravo, O. A. 2004. **Évaluation directe de la compétitivité et de la tolérance à la défoliation des graminées vivaces.** Can. J. Plant Sci. **84**: 195–204. *Stipa clarazii* est une graminée de transition vivace tardive mais dominante dans les exclos ou les grands parcours peu fréquentés des régions semi-arides de l'Argentine, où les vivaces de transition *S. tenuis* et *S. ambigua* peuplent plus hâtivement les buttes de tourbe. Des études récentes indiquent que les espèces de transition tardives sont plus compétitives et tolèrent autant ou mieux les herbivores que les espèces de transition plus précoces. Les auteurs ont formulé les hypothèses suivantes : (1) les plants de *S. clarazii* défoliés tolèrent plus la défoliation que ceux de *S. tenuis* et de *S. ambigua*; (2) *S. clarazii* est plus compétitive que les deux autres espèces quand ses plants ne sont pas défoliés ou sont exposés à une défoliation analogue; (3) la compétitivité de *S. clarazii* diminue quand on défolie cette espèce de manière sélective près de peuplements de *S. tenuis* et de *S. ambigua*. L'étude devait servir à mesurer directement la compétitivité et la tolérance à la défoliation des trois graminées vivaces, cultivées en isolement ou dans des milieux différents puis exposées à divers modes de défoliation observés sur le terrain. En 1998, les auteurs ont tenu deux études parallèles sur un champ de deux ans exclos durant la période végétative. Dans la première, ils ont évalué la réaction des plants défoliés et normaux des trois espèces en l'absence de plantes voisines. Dans la seconde, ils ont sélectionné quatre types d'environnement, de telle sorte que les plantes d'une espèce (cible) était entourée de cinq plants d'une espèce différente. Trois modes de défoliation ont ensuite été appliqués à chaque environnement. Les résultats ont amené les auteurs à retenir les deux premières hypothèses et à rejeter la troisième. Quand les plantes poussent sans voisin immédiat, un meilleur taux de croissance relatif pour la hauteur, une plus forte production de matière sèche et un plus grand nombre de talles filles en fin de saison concourent à une meilleure repousse de *S. clarazii*, comparativement à *S. tenuis* et à *S. ambigua*. La proportion d'atomes ¹⁵N en excédent était toujours plus élevée chez *S. clarazii* que chez les deux autres espèces, sans égard au type d'environnement ou au mode de défoliation. L'absorption du ¹⁵N chez *S. clarazii* était néanmoins semblable à celle observée chez *S. tenuis* ou *S. ambigua* quand on défolie sélectivement *S. clarazii* dans un peuplement non défolié d'une des deux autres espèces. On doit surtout la substitution de *S. clarazii* par des graminées vivaces de transition plus hâtives et moins désirables dans les grands parcours de l'Argentine à un broutage sélectif plutôt qu'à d'autres facteurs comme la compétitivité et la tolérance à la défoliation de l'espèce.

Mots clés: ¹⁵N, parcours d'Argentine, biomasse, absorption d'azote, substitution des espèces, *Stipa*

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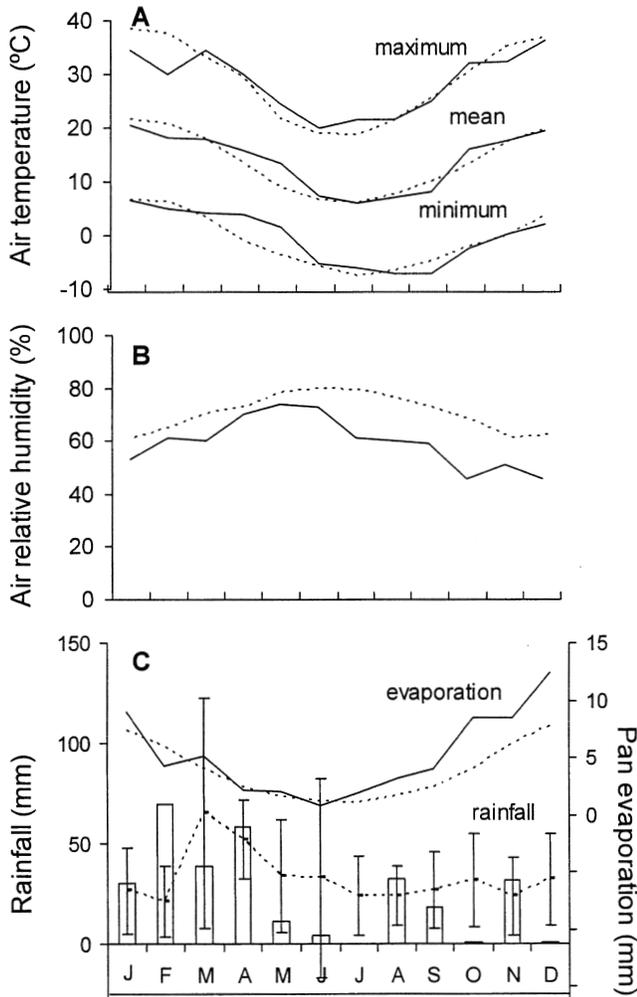


Fig. 1. (a) Absolute monthly maximum and minimum, and mean monthly air temperatures, (b) mean monthly relative humidities and (c) mean monthly pan evaporation and monthly rainfall (1998: histograms; long-term: symbols \pm 1 standard deviation) during 1988–1998 (dotted line) and 1998 (solid line) at a meteorological station located at the study site.

Stipa clarazii (Ball), *S. tenuis* (Phil) and *S. ambigua* (Speg) are abundant C_3 perennial grass species in semiarid, temperate rangelands of central Argentina (Giorgetti et al. 1997). *Stipa clarazii* can be found within exclosures and in areas that have been exposed to moderate and intermittent grazing (Busso 1997). Under these management conditions, desirable (preferred) species for grazing domestic livestock such as *S. clarazii* and *S. tenuis* can replace undesirable (non-preferred) species like *S. ambigua* in rangelands of the south of the phytogeographical province of the Monte (Cano 1988; Giorgetti et al. 1997). However, *S. clarazii* can be replaced by *S. tenuis* under continuous and moderate grazing, and both species are replaced by the undesirable *S. gynerioides* Phil in overgrazed areas (Busso 1997).

Stipa clarazii has been considered one of the more abundant species of the herbaceous layer in the pristine vegetation of rangelands of central Argentina (Busso 1997). This

suggests that *S. clarazii* is a late-seral species. In addition, Moretto (1998) demonstrated a greater competitive ability in *S. clarazii* compared with the undesirable *S. trichotoma* (Nees) or *S. gynerioides* under field and greenhouse conditions. Recent studies have demonstrated that late-seral species can have either similar or greater herbivory tolerance than earlier-seral species due to rapid photosynthetic canopy re-establishment after defoliation (Anderson and Briske 1995). In spite of this, selective defoliation of late-seral species (with greater competitive ability) would be the dominant mechanism in the replacement process of these species by earlier-seral species (with lower competitive ability) (Briske 1991; Anderson and Briske 1995). Selective herbivory is due to a different expression of avoidance mechanisms in plant species, which minimizes the frequency and/or intensity of defoliation because of a reduction in tissue palatability and/or accessibility (Briske 1991).

Anderson and Briske (1995) evaluated the competitive relationships between perennial grasses and the relative contribution of avoidance or tolerance mechanisms to the competitive response by using different neighbourhoods in a transplant garden. When defoliation was applied to both target (a late-seral perennial grass) and neighbouring (conspecifics or mid-seral perennial grasses) species using a similar frequency and intensity, a greater photosynthetic leaf area re-establishment was crucial in determining competitive success. This parameter is an expression of the contribution of tolerance mechanisms to herbivory. These authors studied the influence of selective herbivory by defoliating only the desirable, late-seral species but not its less desirable neighbours. Studies involving plant species of different successional stages and exposed to various defoliation patterns in different neighbourhoods are lacking under field conditions. In addition, mechanistic insight into defoliation competition interactions is scarce, since competition is often inferred indirectly from plant performance, rather than from a direct measurement of resource acquisition (Caldwell et al. 1985).

The objectives of this study were to obtain a direct measure of competitive ability and tolerance to defoliation in *S. clarazii*, *S. tenuis* and *S. ambigua* when these species grew either in different neighbourhoods or in isolation and were exposed to various defoliation patterns under field conditions. Understanding the mechanisms responsible for vegetation changes will allow the prediction of future vegetation change and modelling of how changes in management may influence plant communities. Tolerance to defoliation was estimated through measuring various parameters that affect the speed of photosynthetic surface area re-establishment and dry weight production after defoliation. These parameters included growth rate and relative growth rates for tiller height and length as well as daughter tiller production. Competitive ability was determined by quantifying the amount of ^{15}N in shoots after this N isotope was injected into the soil between the central (target) plant and its nearby neighbour. Hypotheses were that (1) tolerance to defoliation is greater on defoliated plants of *S. clarazii* than on those of *S. tenuis* and *S. ambigua*, (2) competitive ability is greater in *S. clarazii* than in *S. tenuis* and *S. ambigua* when plants remain undefoliated or are exposed to a compara-

Table 1. Number of daughter tillers per parent tiller ($n = 16$ tillers; last sampling date on Dec. 4), total dry weight production per basal area ($n = 4$ plants) and growth rates for green tiller (blade + stem + sheaths) ($n = 12$; average values from Sep. 13 to Dec. 4) on plants of *S. clarazii*, *S. tenuis* and *S. ambigua* that were either defoliated or not during the 1998 study period

Species	Daughters per parent tiller (no. of daughters)		Total dry weight (g cm ⁻²)		Growth rates for green tiller (blade + stem + sheaths) ² (cm d ⁻¹)	
	μ^y	SE ^x	μ	SE	μ	SE
<i>Undefoliated</i>						
<i>S. clarazii</i>	2.25a	0.28	0.126ab	0.048	-0.282a	0.079
<i>S. tenuis</i>	0.62b	0.24	0.051a	0.018	-0.176a	0.096
<i>S. ambigua</i>	0.44b	0.22	0.274b	0.076	-0.069a	0.078
<i>Defoliated</i>						
<i>S. clarazii</i>	1.75a	0.41	0.174a	0.016	0.199b	0.065
<i>S. tenuis</i>	0.94a	0.29	0.059b	0.018	0.142b	0.055
<i>S. ambigua</i>	1.31a	0.38	0.310c	0.024	0.110a	0.054

²Negative rates indicate a negative balance between growth and senescence of green tissue.

^yMean.

^xStandard error.

a-c Means for daughters per parent tiller and total dry weight within columns and defoliation treatments followed by a different letter are statistically different ($P < 0.05$). Means for growth rates for green tiller (blade + stem + sheaths) within the same species followed by a different letter are statistically different ($P < 0.05$).

ble defoliation intensity, and (3) competitive ability decreases in *S. clarazii* when this species is selectively defoliated within a non-defoliated, nearby neighbourhood of *S. tenuis* or *S. ambigua*.

Results of this research will contribute to a better understanding of the species replacement process in the semiarid rangelands of central Argentina. Experimental designs including neighbourhoods, concurrently with resource manipulation and studies to determine competitive ability and interactions among plants, shed light on questions about mechanisms, intensity and consequences of plant interactions under different environmental conditions within a population (Aarssen and Epp 1990).

MATERIALS AND METHODS

Study Site

This study was conducted during 1998 within a 2-yr-old enclosure of domestic herbivory in the Chacra Experimental de Patagones, south of Buenos Aires province (40°39'S, 62°54'W) and within the phytogeographical province of the Monte (Cabrera 1976). Mean monthly temperature, air relative humidity, pan evaporation and rainfall during 1988–1998, and values for these parameters during the study period (May to December 1998) are shown in Fig. 1. Mean annual rainfall in 1998 was 295.6 mm and long-term annual rainfall (1988–1998) was 385 mm.

The soil type is a typical haplocalcid, with an A horizon having a loamy-clay-sandy texture; 0.20 m deep; 1.69% organic carbon, 28.7 ppm available phosphorus, 0.123% total nitrogen. A B_w horizon was found below 0.20 m of soil depth followed by a BC_k horizon between 0.28 and 0.43 m depth. A C_k horizon existed below 0.43 m with very scarce roots. Average pH was 7.

Labour and budget constraints made replication of this study in space and time impossible. Despite the fact that emphasis is

placed on statistical differences, caution is called for extrapolating the results of this study. These should be better viewed under the specific conditions they were obtained.

Treatments and Measurements on Plants Growing without Neighbours

A total of 24 plants each of *S. clarazii*, *S. tenuis* and *S. ambigua*, which had no neighbours within a radius of more than 0.5 m, were randomly selected on May 22 to evaluate the rate of leaf area re-establishment after either 1 or 2 defoliations. This was accomplished by measuring various growth parameters on marked tillers. On each plant, circumference at the soil surface was measured using a steel tape, total (green + dead) and green tiller numbers were counted, and 4 parent tillers were identified by placing wire loops at the stem bases. Half of all plants (12 on each species) were defoliated by clipping to 5 cm stubble height on Sep. 17 (apical meristems were not removed) and Oct. 12 (apical meristems in the reproductive stage of development were removed) while the other half remained undefoliated (controls). Total green and green + dry tiller (blade + stem + sheaths) length, tiller height and daughter tiller production were measured on parent tillers at the initiation of the study (Sep. 13), 6–10 d after the first defoliation (Sep. 26), a few days before the second defoliation (Oct. 7), 6–10 days after the second defoliation (Oct. 23), and at the end of the growing cycle (Dec. 4). Four plants of each species and defoliation treatment were destructively harvested for other experimental purposes (see Saint Pierre et al. 2004) in late September and October and in early December. Regrowth production was measured on defoliated plants at these dates.

Growth rates (GR , cm d⁻¹) were calculated as $GR = (V_{t+i} - V_t)/i$ (Radford 1967) where V is the plant variable, t is initial time (days) and i is the time increment (days). Relative growth rates (cm cm⁻¹ d⁻¹) were calculated for length and height measurements following the previous formula except that lognormal V was used rather than V .

Table 2. Dry weight production ($n = 4$, regrowth, g cm^{-2}) per basal area basis on defoliated plants of *S. clarazii*, *S. tenuis* and *S. ambigua* at the first (Sep. 26), second (Oct. 23) and third sampling dates (Dec. 4) after 9, 36 and 78 d of regrowth, respectively. Plants harvested at the first sampling date were exposed to one defoliation on Sep. 17 while those harvested at the second and third sampling dates were exposed to defoliation on Sep. 17 and Oct. 12.

Species	Sep. 26		Oct. 23		Dec. 4	
	μ^z	SE ^y	μ	SE	μ	SE
<i>S. clarazii</i>	0.001a	0.0004	0.009a	0.0036	0.042a	0.0159
<i>S. tenuis</i>	0.003a	0.0011	0.002b	0.0007	0.019a	0.0085
<i>S. ambigua</i>	0.003a	0.0010	0.001b	0.0003	0.010a	0.0051

^zMean.

^yStandard error.

a–b Means within columns followed by a different letter are statistically different ($P < 0.05$).

Aboveground 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 non-defoliated plants during the whole study period, as well as 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. Comparison of dry weight production per plant was prevented because of inherent plant basal area variation among species. Therefore, dry weight production data are reported per basal area basis. All plant tissues obtained above clipping height were oven-dried at 60°C for 48 h and then weighed. Current-year live and recently dead material were separated from older, previous-year tissues, which had a grey colour. This separation based on leaf colour was clear and reliable and it has been reported in other studies on perennial grasses (Busso et al 2001).

Treatments and Measurements on Plants Growing with Neighbours

Four different types of neighbourhoods were selected in the field within a 6 ha enclosure to a domestic herbivory on May 27 and Jun. 9 at the beginning of the 1998 growing season. Neighbourhoods were completely randomized within the field. Each neighbourhood type consisted of a central plant (target) of one species surrounded by five neighbouring plants of a different species. They were (1) target = *S. clarazii*, neighbours = *S. ambigua*; (2) target = *S. tenuis*, neighbours = *S. ambigua*; (3) target = *S. clarazii*, neighbours = *S. tenuis*; and (4) target = *S. tenuis*, neighbours = *S. clarazii*. *Stipa ambigua* was not included as a target species because it is not often consumed by livestock (Cano 1988). Three defoliation patterns were imposed on each neighbourhood type: (1) both target and neighbours remained undefoliated (control), (2) only the target, but not the neighbours, was defoliated, and (3) both target and neighbours were defoliated. Defoliation was effected by clipping, leaving 5-cm stubble height on Sep. 19 and Oct. 12. All plants were harvested at clipping height at the end of the study on Nov. 22. All plants in each neighbourhood within a radius of 1.5 m from the target were first clipped leaving 5-cm stubble and then maintained to this clipping height to reduce com-

petitive effects from surrounding vegetation. Six replicates were used per treatment so that 72 neighbourhoods were initially marked (three defoliation patterns \times four neighbourhood types \times six replicates per treatment).

For each neighbourhood type, the target and its five neighbours were identified. Basal circumference was measured using a steel tape and total (green + dry) tiller number was counted for each plant. Distances from neighbour to target edges were also taken. Mean distance between the target and its closest neighbour was 9.49 ± 0.68 cm ($n = 72$). The remaining, more distant neighbours within any neighbourhood were at a distance of 21.49 ± 0.56 cm ($n = 282$) from the target. Aboveground dry weight production per basal area was obtained as previously discussed. Growth rates during 19 Sep. to 22 Nov. were calculated by dividing the total dry weight produced during this period by the number of days of such a period. Plant basal area was calculated from circumference measurements.

Acquisition of ^{15}N from the soil equidistant between a target plant and its closest neighbour was evaluated in six randomly selected target–closest neighbour pairs within each of the neighbourhood types and patterns of defoliation. Pulses of nitrogen isotope consisted of 100 mL of a 35 mM $^{15}(\text{NH}_4)_2\text{SO}_4$ solution containing 60% ^{15}N excess. They were injected into soils to a depth of 10 cm with a syringe on 19 September 1998. Harvested biomass was dried at 60°C for 48 h and ground to pass through a 40-mesh screen. Percentage total N was determined using a modified Kjeldahl method (Fiedler and Proksch 1975). The $^{14}\text{N}/^{15}\text{N}$ ratio was obtained after exposing the samples to the Rittenberg oxidation (Rittenberg 1948) using an emission spectrometer NO16 PC (National Commission of Atomic Energy, Ezeiza, Buenos Aires). Mean ($n = 12$) background ^{15}N atom percentage values ($0.37\% \pm 0.002$) were subtracted from labelled samples to determine ^{15}N atom percentage excess values. ^{15}N samples were collected from undefoliated plants at the end of the season when aboveground biomass was harvested. Pools of ^{15}N were calculated by multiplying the shoot mass, percentage shoot nitrogen and ^{15}N atom percentage excess of harvested shoot tissues.

Statistical Analysis

All variables were analysed using one- or two-way ANOVA using a completely randomised experimental design. Values of ^{15}N atom percentage excess were square-root transformed. Untransformed data are presented in tables and figures. Means of the studied parameters were compared using Fisher's Least Significance Difference test at the 5% level when F -tests indicated that a variable was significant at the 0.05 level (Steel and Torrie 1981).

RESULTS

Plant basal area was similar ($P > 0.05$) among species when they grew without neighbours. Mean values were 53.9 ± 5.7 cm^2 , 72.5 ± 6.3 cm^2 , and 111.2 ± 15.2 cm^2 in *S. clarazii*, *S. tenuis* and *S. ambigua*, respectively. However, plant basal area of plants that grew with neighbours differed ($P < 0.05$) across treatments from 16.5 to 105.8 cm^2 . Average values were 25.56 ± 2.1 cm^2 in *S. clarazii*, 40.93 ± 3.1 cm^2 in

S. tenuis and $78.71 \pm 5.7 \text{ cm}^2$ in *S. ambigua*. This difference among species was partially due to inherent species differences in plant size. Because of this, plant responses are presented on a per plant basal area basis to facilitate comparisons between and across treatments. Nevertheless, target and closest neighbour did not differ ($P > 0.05$) in basal area within any neighbourhood type.

Plants which Grew without Neighbours

Components of Leaf Area Production and Dry Weight Production

Total tiller density at the beginning of the study ($n = 148$) was greater ($P < 0.05$) in *S. tenuis* (3.8 ± 0.2 tillers cm^{-2}) than in *S. clarazii* (2.9 ± 0.2) and *S. ambigua* (2.5 ± 0.1). Proportion of green tillers to total tiller number per plant was similar ($P > 0.25$) in all three species, and they were 0.61 ± 0.02 in *S. clarazii*, 0.65 ± 0.02 in *S. tenuis* and 0.64 ± 0.02 in *S. ambigua*. Daughter tiller production was greater ($P < 0.05$) on undefoliated plants of *S. clarazii* than on those of *S. tenuis* and *S. ambigua* during the study period (Table 1). Total dry weight production at the end of the growing season was more than twice as much on defoliated and undefoliated plants of *S. ambigua* as on those of the other 2 species (Table 1). Defoliated plants showed a similar ($P > 0.35$) total dry weight production as undefoliated controls in all three species.

Dry weight production after defoliation (regrowth) was similar or greater ($P < 0.05$) in *S. clarazii* than in *S. tenuis* and *S. ambigua* (Table 2). Total (green + dry) tiller (blades + stem + sheaths) length and tiller height on undefoliated plants were greater in *S. ambigua* than in *S. clarazii* and *S. tenuis* (Fig. 2). However, relative growth rates for height and rates of dry weight production were greater ($P < 0.05$) in *S. clarazii* ($0.027 \pm 0.005 \text{ cm cm}^{-1} \text{ d}^{-1}$ and $0.0172 \pm 0.0052 \text{ g cm}^{-2} \text{ d}^{-1}$, respectively) than in *S. tenuis* ($0.012 \pm 0.003 \text{ cm cm}^{-1} \text{ d}^{-1}$ and $0.0075 \pm 0.0021 \text{ g cm}^{-2} \text{ d}^{-1}$, respectively) and *S. ambigua* ($0.007 \pm 0.001 \text{ cm cm}^{-1} \text{ d}^{-1}$ and $0.0051 \pm 0.0018 \text{ g cm}^{-2} \text{ d}^{-1}$, respectively).

Growth rates of green tillers (blade + stem + sheaths) were greater ($P < 0.05$) on defoliated than on undefoliated plants in *S. clarazii* and *S. tenuis* (Table 3).

Plants Growing in Competition with Neighbours

Dry Weight Production

From Sep. 19 to Nov. 22, production of dry weight after defoliation was greater ($P < 0.05$) on defoliated plants of *S. clarazii* ($0.046 \text{ g DM cm}^{-2} \pm 0.0065$) than on those of *S. tenuis* ($0.021 \text{ g DM cm}^{-2} \pm 0.0036$) and *S. ambigua* ($0.018 \text{ g DM cm}^{-2} \pm 0.0022$). Toward the end of the study, total dry weight production was greater ($P < 0.05$) on the target *S. clarazii* than on its *S. tenuis* neighbours for any defoliation treatment (Table 4, Fig. 3c). Production of total dry weight per square centimeter was greater in *S. clarazii* than in *S. tenuis* by 53–131% when all plants remained undefoliated, by 73–253% when only the target *S. clarazii* was defoliated or 74–213% when all plants were defoliated (Fig. 3c). Undefoliated *S. clarazii* and *S. tenuis* showed a similar ($P > 0.05$) total dry weight production when *S. tenuis*

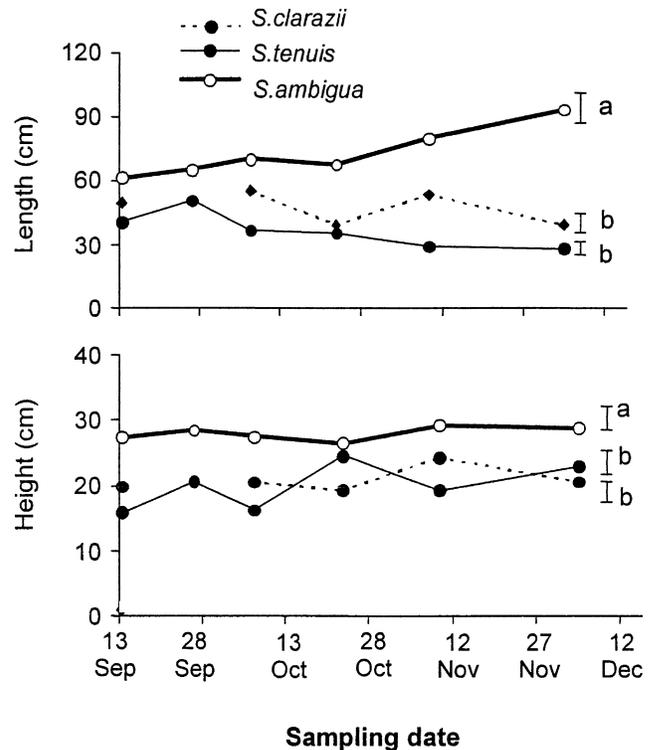


Fig. 2. Green + dry (blade + stem + sheath) length and height on tillers of undefoliated plants of *S. clarazii*, *S. tenuis* and *S. ambigua* during the 1998 study period. Each symbol is the mean of $n = 14$ –48 tillers. Vertical bars indicate \pm an average of the SE of the means. For the last sampling date, means followed by different letters are statistically significant ($P < 0.05$).

was surrounded by neighbours of *S. clarazii* (Table 4, Fig. 3d). However, total dry weight production was lower ($P < 0.05$) in *S. tenuis* than in *S. clarazii* when either *S. tenuis* or *S. tenuis* and *S. clarazii* were defoliated in this neighbourhood (Fig. 3d).

Total dry weight production was similar ($P > 0.19$) on defoliated and undefoliated plants in *S. ambigua* when this species grew in competition with *S. tenuis* (Fig. 3b). However, *Stipa tenuis* showed a lower ($P < 0.01$) total dry weight production whenever this species was surrounded by defoliated or undefoliated neighbours of *S. ambigua* (Fig. 3b). Average growth rates were $0.0001 \text{ g cm}^{-2} \text{ d}^{-1}$ in *S. tenuis* and more than three times this value were observed in *S. ambigua*. Also, total dry weight production was greater on defoliated ($P < 0.05$) than on undefoliated plants in *S. ambigua* when the target species was *S. clarazii* (Table 4, Fig. 3a).

¹⁵N Uptake

The pool of ¹⁵N atom excess was greater ($P < 0.05$) in target plants of *S. clarazii* than in *S. ambigua* neighbours when all plants remained undefoliated (Table 5). Even though ¹⁵N atom excess pools were greater in *S. clarazii* than in *S. ambigua*, values did not differ significantly ($P > 0.05$) between these species when only *S. clarazii* or both species

Table 3. Analysis of variance examining the effects of the defoliation patterns (undefoliated, only the target defoliated, both target and neighbour defoliated) and neighbourhood type (target and neighbours from 1 to 5) on total aboveground dry matter production per basal area

		df	Mean squares
Target: <i>S. clarazii</i>	Pattern of defoliation	2	0.1499**
Neighbours: <i>S. ambigua</i>	Neighbourhood type	5	0.0191 NS
	Interaction	10	0.0371 NS
	Error	90	0.0254
Target: <i>S. tenuis</i>	Pattern of defoliation	2	0.0431 NS
Neighbours: <i>S. ambigua</i>	Neighbourhood type	5	0.2775***
	Interaction	10	0.0078 NS
	Error	90	0.0256
Target: <i>S. clarazii</i>	Pattern of defoliation	2	0.2161***
Neighbours: <i>S. tenuis</i>	Neighbourhood type	5	0.1328***
	Interaction	10	0.0271 NS
	Error	90	0.0236
Target: <i>S. tenuis</i>	Pattern of defoliation	2	0.1680***
Neighbours: <i>S. clarazii</i>	Neighbourhood type	5	0.0372 NS
	Interaction	10	0.0159 NS
	Error	90	0.0182

*, **, *** Significant at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively; NS, not significant, $P > 0.05$.

Table 4. ^{15}N atom excess in shoots of *Stipa clarazii*, *S. tenuis* and *S. ambigua* under different defoliation patterns in different neighbourhoods at the end of the growing season

Neighbourhood	Control		Only target defoliated		Both target and neighbours defoliated	
	^{15}N atom excess SE ^z		^{15}N atom excess SE		^{15}N atom excess SE	
	(mg cm ⁻²)					
<i>S. clarazii</i> (target)	0.081a,ab	0.016	0.132a,a	0.062	0.038a,b	0.007
<i>S. ambigua</i> (neighbour)	0.032b,a	0.014	0.090a,b	0.026	0.029a,a	0.006
<i>S. tenuis</i> (target)	0.040a,a	0.016	0.011a,a	0.004	0.012a,a	0.004
<i>S. ambigua</i> (neighbour)	0.060a,a	0.024	0.057b,a	0.024	0.022a,a	0.010
<i>S. clarazii</i> (target)	0.0995a,a	0.016	0.177a,a	0.037	0.126a,a	0.052
<i>S. tenuis</i> (neighbour)	0.049a,a	0.007	0.195a,b	0.044	0.040b,a	0.019
<i>S. tenuis</i> (target)	0.102a,a	0.036	0.070a,a	0.019	0.064a,a	0.012
<i>S. clarazii</i> (neighbour)	0.167a,a	0.051	0.133a,a	0.010	0.219b,a	0.041

^zStandard error.

a–b Within a same column and neighbourhood, different letters to the left of the comma indicate significant ($P < 0.05$) differences between species within each defoliation pattern. Within a same row, different letters to the right of the comma indicate significant ($P < 0.05$) differences between defoliation patterns within each species.

were defoliated (Table 5). *Stipa ambigua* showed greater ($P < 0.05$) pools of ^{15}N atom excess when *S. clarazii* was selectively defoliated than when both species were exposed to a similar defoliation intensity or remained undefoliated (Table 5).

Pools of ^{15}N were similar in plants of *S. tenuis* and *S. ambigua* when these species were both defoliated or remained undefoliated (Table 5). However, undefoliated plants of *S. ambigua* had a greater ($P < 0.05$) pool of ^{15}N atom excess when *S. tenuis* was selectively defoliated. Within each of these species, there was no effect of the defoliation pattern on the pool of ^{15}N atom % excess.

Selectively defoliated plants of *S. clarazii* had a similar or greater ($P < 0.05$) ^{15}N atom excess pool than *S. tenuis* when this latter species was either defoliated or not (Table 5). The different defoliation patterns had no effect on the ^{15}N atom excess pool in *S. clarazii*. However, ^{15}N atom excess pools in *S. tenuis* were greater ($P < 0.05$) when *S. clarazii* was selectively defoliated than when both species remained

undefoliated or were exposed to a similar defoliation intensity. When *S. tenuis* was the target species, *S. clarazii* always showed greater ^{15}N atom excess pools although differences were only significant ($P < 0.05$) when plants of both species were defoliated (Table 5). In this neighbourhood, patterns of defoliation had no effect ($P < 0.60$) on ^{15}N atom excess pools within each species.

Percentage N of regrowth was similar or higher ($P < 0.05$) in *S. clarazii* than in *S. tenuis* in all neighbourhoods composed of these two species (Table 6). Between Oct. 12 and Nov. 22, *S. clarazii* showed a greater ($P < 0.05$) percentage N or ^{15}N atom excess content than *S. ambigua* or *S. tenuis*, respectively, in regrowth foliage (Table 6).

DISCUSSION

When plants grew without nearby neighbours, *S. clarazii* showed greater regrowth following defoliation than *S. tenuis* and *S. ambigua*. Greater relative growth rates for height, and end-of-season daughter tiller production per par-

ent tiller in *S. clarazii* than in the other two species contributed to this response. These results indicate a greater defoliation tolerance in *S. clarazii* than in *S. tenuis* and *S. ambigua*. A rapid photosynthetic surface area re-establishment through production of new tillers and tiller elongation is characteristic of perennial grasses tolerant to defoliation (Caldwell et al. 1981; Briske and Richards 1995; Briske and Hendrickson 1998). In addition, greater growth of any given species may have implications in the capacity for soil resource acquisition. For example, when two perennial grass species (*S. scoparium* and *Paspalum plicatulum* Michx.) grew near each other, the species with greater growth was potentially released from nutrient limitation as a result of lower growth in the other species (Van Auken and Bush 1997). Under these conditions, *S. scoparium* took advantage of unused resources by *P. plicatulum*, which indicated a significant competitive intensity (Van Auken and Bush 1997).

Although only some differences were statistically significant, amounts of ¹⁵N atom excess were always greater in *S. clarazii* than in *S. tenuis* and *S. ambigua* independent of neighbourhood type and pattern of defoliation. The only exception was when *S. clarazii* was selectively defoliated and its nearby *S. tenuis* neighbours remained undefoliated. Under these treatments, pools of ¹⁵N were similar in both species, which led to rejection of the third hypothesis. Pools of ¹⁵N were also greater on regrowth of *S. clarazii* than on that of *S. tenuis* and *S. ambigua*. However, differences were significant only when target plants of *S. tenuis* were surrounded by *S. clarazii* neighbours. Greater N absorption in *S. clarazii* than in *S. tenuis* and *S. ambigua* would suggest that *S. clarazii* is a superior competitor compared with the other two species. Greater defoliation tolerance in *S. clarazii* could partially be explained through its greater competitive ability since nutrient uptake is positively related to growth rate (Grime 1979; Fitter and Hay 1983). Similar results were reported by Anderson and Briske (1995) in *Schizachyrium scoparium*: late-seral species showed a similar or greater defoliation tolerance than earlier-seral species.

When plants grew in isolation, total dry weight production at the end of the growing season was greater on defoliated and undefoliated plants of *S. ambigua* than in the other two species. Initial biomass was the main determinant of this result because dry weight accumulated at the time of the first defoliation was more than 75% of total dry weight production on defoliated plants of the three species. In addition, daughter tiller production (Table 1) was greater in *S. clarazii* than in *S. ambigua*. A greater green + dry blade + stem + sheath length and height (Figure 2) on undefoliated tillers occurred in *S. ambigua* than in the other two species. This was, therefore, more important than daughter tiller production for explaining the observed responses in total dry weight production.

Growth rates for green blade + stem + sheaths in *S. clarazii* and *S. tenuis* were greater on defoliated than on undefoliated tillers on plants growing without nearby neighbours (Table 3). This most likely contributed to a similar ($P > 0.89$) total dry weight production in both defoliation treatments at the end of the study period. Becker et al. (1997)

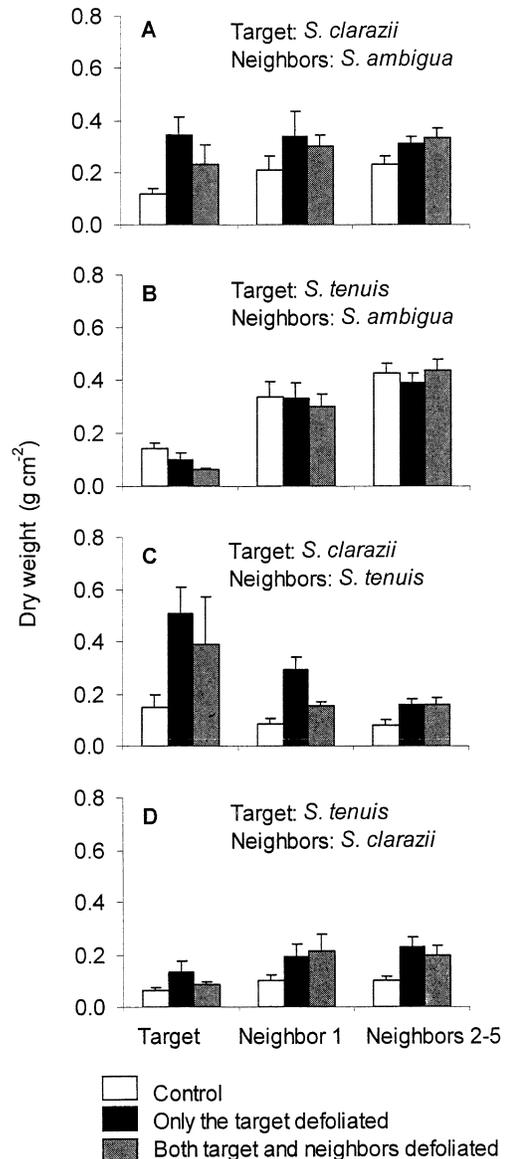


Fig. 3. Total dry weight production per basal area of plants of *S. clarazii*, *S. tenuis* and *S. ambigua* exposed to different defoliation patterns (Control = all plants remained undefoliated; only the target was defoliated; both target and neighbours were defoliated) under various neighbourhood types (indicated at the top of panels). Target refers to an individual of any species surrounded by neighbours of another species. Neighbour 1 is always the closest to the target. Each histogram is the mean \pm 1 SE of $n = 6$.

also obtained a similar dry weight production on plants of *S. tenuis* that remained undefoliated or that were defoliated at different stages of internode elongation under natural conditions. The results from this study agree with those observed by Flemmer (2000) when *S. clarazii* and *S. tenuis* were either defoliated or not at different phenological stages in competition with undefoliated plants of *S. gynerioides* under rainfed conditions. In Flemmer's study, however, dry weight production was more than 26% lower on defoliated than on undefo-

Table 5. Percentage N and ^{15}N atom excess content ($n = 6$) in regrowth of *Stipa clarazii*, *S. tenuis* and *S. ambigua* which grew in various neighbourhoods where the target plant (T) and its closest neighbour (N) were defoliated

Date	Neighbourhood	% N		^{15}N atom excess (mg cm^{-2})	
		μ^z	SE ^y	μ	SE
Sep. 19 – Oct. 12	<i>S. clarazii</i> (T)	2.52a	0.10	0.006a	0.002
	<i>S. ambigua</i> (N)	2.31a	0.09	0.003a	0.001
	<i>S. tenuis</i> (T)	2.25a	0.11	0.002a	0.001
	<i>S. ambigua</i> (N)	2.01a	0.11	0.002a	0.001
	<i>S. clarazii</i> (T)	2.46a	0.04	0.009a	0.003
	<i>S. tenuis</i> (N)	1.84b	0.11	0.007a	0.005
	<i>S. tenuis</i> (T)	1.96a	0.07	0.014a	0.004
	<i>S. clarazii</i> (N)	3.24b	0.42	0.020a	0.008
Oct. 12 – Nov. 22	<i>S. clarazii</i> (T)	2.64a	0.09	0.019a	0.005
	<i>S. ambigua</i> (N)	1.90b	0.16	0.011a	0.002
	<i>S. tenuis</i> (T)	2.15a	0.14	0.004a	0.001
	<i>S. ambigua</i> (N)	2.02a	0.12	0.011a	0.005
	<i>S. clarazii</i> (T)	2.35a	0.06	0.069a	0.034
	<i>S. tenuis</i> (N)	2.22a	0.07	0.016a	0.007
	<i>S. tenuis</i> (T)	1.84a	0.12	0.023a	0.004
	<i>S. clarazii</i> (N)	2.22b	0.13	0.113b	0.045

^zMean.^yStandard error.a–b Within the same column and neighbourhood, different letters indicate significant ($P < 0.05$) differences between species within each regrowth period.

liated plants of *S. clarazii* and *S. tenuis* when these species grew in competition with undefoliated *S. gynerioides* under irrigation. Under irrigation, greater biomass of *S. gynerioides* caused photosynthetically active radiation to the stem bases of *S. clarazii* and *S. tenuis* to be on average 74% lower than in the rainfed or water stress treatment (Flemmer et al. 1998). Defoliation of these desirable grasses under good conditions of soil water availability and when in competition with undesirable, undefoliated perennial grasses could thus speed up ecological system degradation.

Total dry weight production was lower ($P < 0.01$) in *S. tenuis* whenever this species was surrounded by neighbours of *S. ambigua* (Fig. 3b). Results obtained for *S. ambigua* in this study are striking in a species that owes its grazing resistance mainly to avoidance mechanisms. This species is defoliated only when a better forage is not available (Cano 1988). Low palatability in *S. ambigua* could partially be explained by its high lignin (mean = 9.4%) and low crude protein (mean = 8.9%) concentrations in comparison to lignin (5.5%) and crude protein (13.7%) values observed in the palatable species *S. clarazii* (H. D. Giorgetti, O. A. Montenegro and G. D. Rodríguez, unpublished data). It was also observed that regrowth produced from Oct. 12 to Nov. 22 had a lower percentage nitrogen in *S. ambigua* than in *S. clarazii* (Table 6). A negative correlation between production of secondary compounds and leaf growth is often assumed (Skogsmyr and Fagerström 1992; Loehle 1996). However, a tradeoff between avoidance mechanisms and defoliation tolerance was not evident in the undesirable *S. ambigua*.

Dry weight production was greater in the target *S. clarazii* than in its *S. tenuis* neighbours for any defoliation treatment. Greater ^{15}N uptake in *S. clarazii* than in *S. tenuis* can contribute to explain this plant response. Fitter and Hay (1983) reported a direct, positive relationship between nutrient uptake and

growth rate. However, pools of ^{15}N in *S. tenuis* were greater only when the target *S. clarazii* was selectively defoliated than when both species remained undefoliated or were exposed to a similar defoliation intensity. This suggested that undefoliated plants of *S. tenuis* took advantage of competitive release after *S. clarazii* was selectively defoliated.

Greater competitive ability and defoliation tolerance in *S. clarazii* than in *S. tenuis* and *S. ambigua* would place *S. clarazii* as a dominant species in well-managed grasslands. At the study site, percentage contribution to total perennial grass biomass increased from 3.4 to 14.6% in *S. clarazii* and decreased from 27.5 to 13.1% in *S. ambigua* in areas that were excluded from domestic herbivory and that had not been exposed to any disturbance during a 9-yr period (Giorgetti et al. 1995). At the same time, plant frequency increased from 7.5 to 15% in *S. clarazii* and decreased from 65 to 32.5% in *S. ambigua* (Giorgetti et al. 2000). Selective and continuous defoliation of *S. clarazii*, however, would lead to its replacement by other, comparatively less preferred species like *S. tenuis* and eventually by the unpreferred, unpalatable *S. ambigua*. This implies that selective herbivory can suppress competitive ability of the dominant species and change the competitive advantage toward subordinate, less competitive species. The characteristics of defoliation (i.e., intensity, frequency, timing) that lead to changes in competitive advantage from the dominant to the subordinate species would represent the resistance threshold to herbivory that must be exceeded previous to the occurrence of changes in the species composition of the community (Briske 1996).

Selective herbivory of *S. clarazii*, rather than factors associated with its competitive ability and defoliation tolerance, would be the major factor driving its replacement by less desirable perennial grasses in rangelands of central Argentina.

Anderson and Briske (1995) arrived at a similar conclusion for *Schizachyrium scoparium*. However, the influence of selective herbivory on the intensity and duration of competitive interactions could be minimized under conditions of low or unpredictable resource availability (Grime 1979). Other plant characteristics, in addition to vegetative growth, could also be affected by herbivory intensity and duration, and then act as variables in the species replacement process within a plant community. For example, continuous defoliation could reduce sexual reproduction in some species thereby affecting plant demography and community composition (O'Connor 1991).

CONCLUSIONS

This study demonstrated a greater competitive ability and defoliation tolerance in *S. clarazii* than in *S. tenuis* and *S. ambigua*, which would place *S. clarazii* as a dominant species in well-managed rangelands. Conclusions of this study may be similar on a different soil or on a soil with a different fertility level. Although determined indirectly through biomass measurements, other studies have shown a greater competitive ability and defoliation tolerance in the late-seral *S. clarazii* than in earlier-seral species (Moretto and Distel 1997, 1999). These studies have been conducted under very different fertility levels under either field or greenhouse conditions.

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