Competitive ability of three perennial grasses native to Central Argentina: Demography and dry weight production

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Abstract A measure of competitive ability and tolerance to defoliation was obtained at the field in the desirable, later-seral *Stipa clarazii* and *S. tenuis* and the undesirable, earlier-seral *S. ambigua* through measurements of various growth components and dry matter production in central Argentina (40° 39'S, 62° 54'W). These species are perennial tussock grasses native to Argentinean rangelands. Growth components and dry matter production were measured on defoliated and undefoliated plants of these species growing without nearby neighbors. A parallel study evaluated dry matter production in these species when they grew with different nearby neighboring species and were exposed to various defoliation patterns. Towards the end of the study, the amount of regrowth on plants which grew without nearby neighbors was greater in *S. clarazii* ($\bar{x} \pm 1$ S.E.=0.058± 0.034) than in *S. tenuis* (0.023±0.010) and *S. ambigua* (0.017±0.004). Greater relative growth rates for green blades, stem+sheaths and blade+stem+sheaths, and height, and a greater daughter tiller production in *S. clarazii* than in the other two species contributed to explain this response. Similar results were obtained when dry matter production was evaluated in the different neighborhood types and under different defoliation patterns. These results suggest that *S. clarazii* is a superior competitor when compared to *S. tenuis* and *S. ambigua*. The more competitive species also showed as the more tolerant to defoliation due to its greater daughter tiller production and tillers of fastest growth. Dry matter production was lower ($P<0.01$) in *S. tenuis* whenever this species was surrounded by neighbors of *S. ambigua;* the undesirable *S. ambigua* showed then characteristics of a species more tolerant to defoliation than *S. tenuis*. However, the response in *S. tenuis* differed when plants were grown without nearby neighbors: the similar regrowth production in *S. tenuis* and *S. ambigua* suggests that the desirable species is able to utilize soil resources when they are available and produce a greater growth in absence of nearby competitors. This study demonstrated that later-seral species (i.e., *S. tenuis*) may or may not show a greater competitive ability or tolerance to defoliation than earlier-seral species (i.e., *S. ambigua*). Proximity of nearby neighbors appeared to be a major determinant of the obtained response.

Key words Perennial grasses - Competitive ability - Defoliation - Plant demography- Biomass

Introduction

Stipa clarazii, *S. tenuis* and *S. ambigua* 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 to domestic herbivory and in areas which have been exposed to moderate and intermittent grazing (Distel and Bóo 1996). Under these management conditions, desirable (preferred) species such as *S. clarazii* and *S. tenuis* can replace undesirable (nonpreferred) species like *S. ambigua* in rangelands of the South of the Phytogeographical Province of the Monte (Cano 1988; Giorgetti et al. 1997; H.D. Giorgetti, unpublished data). However, *S. clarazii* can be replaced by *S. tenuis* under continuos and moderate grazing, and both species are replaced by the undesirable *S. gynerioides* in overgrazed areas (Distel and Bóo 1996; Moretto and Distel 1999).

Stipa clarazii has been proposed as one of the more abundant species of the herbaceous layer in the pristine vegetation of rangelands of Central Argentina (Fernández and Distel 1999). This suggests that *S. clarazii* is a late-seral species. Additionally, Moretto and Distel (1997) demonstrated a greater competitive ability in *S. clarazii* than in the undesirable *S. trichotoma* or *S. gynerioides* under field or greenhouse conditions, respectively. Recent studies have demonstrated that late-seral species can have an either similar or greater herbivory tolerance than earlier-seral species due to its rapid photosynthetic canopy reestablishment 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; Moretto and Distel 1999). Selective herbivory is due to a different expression of avoidance mechanisms in plant species, which minimize the frequency and/or intensity of defoliation because of a reduction in tissue palatability and/or accessibility (Briske 1991; Moretto 1998).

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 neighborhoods in a transplant garden. When defoliation was effected on both target (a late-seral perennial grass) and neighboring (conspecifics or mid-seral perennial grasses) species using a similar both frequency and intensity, a greater photosynthetic leaf area reestablishment 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 only defoliating the desirable, late-seral species but not its less desirable neighbors. Studies involving plant species of different successional stages and exposed to various defoliation patterns in different neighborhoods are lacking under field conditions.

Our objective was to obtain a measure of competitive ability and tolerance to defoliation in *S. clarazii*, *S. tenuis* and *S. ambigua* when these species grow either in different neighborhoods or in isolation and are exposed to various defoliation patterns under field conditions. With this purpose, several growth components and dry matter production were evaluated in these species (e.g., see Roush and Raadosevich 1985). Results of this research will contribute to gain a better understanding of the species replacement process in the semiarid rangelands of Central Argentina. Experimental designs including neighborhoods, 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 and species

This study was conducted during 1998 within a two-year-old exclosure to 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). During 1901-1950, mean annual rainfall, mean annual temperature, absolute minimum temperature (August), absolute maximum temperature (January), mean annual relative humidity and mean annual wind speed were 331 mm, 14.6°C, -7.6°C, 43°C, 60% and 13 km h^{-1}, respectively. Rainfall was 295.6 mm in 1998. A meteorological station located at the Chacra Experimental de Patagones provided the climatic parameters shown in Figure 1 during the study period (May to December 1988).

The soil type is a typical haplocalcid, with an A horizon 20 cm deep. This deep soil has a loamy sand texture, 1.69% organic carbon, 28.7 ppm available phosphorus, 0,123% total nitrogen and an average pH of 7.

Fig 1 -

Treatments and measurements on plants without nearby neighbors

A total of 72 plants of *S. clarazii*, *S. tenuis* and *S. ambigua* which had no neighbors within a radius of more than 0.5 m were randomly selected on 22 May to have a measure of the rate of leaf area reestablishment after either one or two defoliations. This was effected by measuring various growth parameters on marked tillers. On each plant, plant circumference at the soil surface was measured, total (green+dead) and green tiller number were counted, and 4 parent tillers were identified by using wire loops at the stem bases. Half of all plants was defoliated by clipping to 5 cm stubble height on 17 September and 12 October while the other half remained undefoliated (control). Height, total green and green+dead blade lengths, total green and green+dead sheath lengths, and daughter tiller production were measured on parent tillers at the initiation of the study (13 September), 6-10 days after the first defoliation (26 September), a few days before the second defoliation (7 October), 6-10 days after the second defoliation (23 October), and at the end of the growing cycle (4 December). Periodically during the study period, four plants of each species and defoliation treatment were destructively harvested with other experimental purposes so that only four plants remained for measurements per species and defoliation treatment at the end of the study.

Growth rates (GR, cm d^{-1}) were calculated as $GR=(V_{t+1} - V_t)/i$ (Radford 1967) were V is the plant variable [blade length (B), stem+sheath length (SSH), total length (B+SSH), height] , *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 *ln*V was used rather than V.

Aboveground dry matter production was measured at the time of the defoliation treatments (**C**, clipping). At the end of the growing cycle, the amount of dry matter produced by nondefoliated 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 harvested. Total dry weight produced by defoliated plants was calculated as **C+R**. All plant tissues obtained above clipping height were oven dry to 60 °C and then weighed.

Treatments and measurements on plants with nearby neighbors

Four different neighborhood types were selected at the field on 27 May and 9 June at the beginning of the 1998 growing season. They were (1) plant of *S. clarazii* (target) surrounded by neighbors of *S. ambigua*; (2) target=*S. tenuis*, neighbors=*S. ambigua*; (3) target=*S. clarazii*, neighbors=*S. tenuis*; (4) target=*S. tenuis*, neighbors=*S. clarazii*. Three different defoliation patterns were imposed on each neighborhood type: (a) both target and neighbors remained undefoliated (control), (b) only the target, but not the neighbors, was defoliated, (c) both target and neighbors were defoliated. Defoliation was effected by clipping, leaving 5 cm stubble height on 19 September (apical meristems were not removed) and 12

October (apical meristems in the reproductive stage of development were removed). All plants were harvested at clipping height on 22 November, at the end of the study. All plants around each neighborhood within a radius of 1.5 m from the target were first clipped and then maintained to clipping height to reduce competitive effects from surrounding vegetation. Six replicates were used per treatment so that 72 neighborhoods were initially marked (3 defoliation patterns x 4 neighborhood types x 6 replicates per treatment).

At each neighborhood type, the target and its 5 nearby neighbors were identified, and basal circumference and total (green+dry) tiller number were obtained for each plant. Distance from neighbors to target was also taken. Aboveground dry matter production was obtained as indicated under the previous heading. Growth rates during 19 September-22 November were calculated by dividing the total dry matter produced during this period by the number of days of such a period. Plant basal area was calculated from circumference measurements.

Statistical analysis

All variables were analyzed using one- or two-way ANOVA. Tukey's test was performed to compare means when F tests indicated that a variable was significant at the 0. 05 level (Steel and Torrie 1981).

Results and Discussion

Plant basal area ($\bar{x}$±1 S.E.: 8.1±1.8-124.5±51.7 cm^2) was highly variable within and among treatments for all species. This prevents us to compare dry matter production on a plant basis. Competitive ability has been shown to increase as plant size increases in several species (Donald 1958; Grime 1979; Keddy 1990). Initial plant size, however, may not affect competitive response within certain ranges of this parameter (Tilman 1988; Taylor et al. 1990). Thus, Scott and Wilson (1994) suggested that it is possible to compare the competitive response among species even though they differ in their initial size. Competitive ability may not simply be the result of differences in plant size at transplanting time but also a consequence of differences in either physiological processes or patterns of carbon distribution within each species (DiTommaso and Aarssen 1991; Wilson and Tilman 1991). In this manner, dry matter production will be reported on a per surface area basis since tiller density (1.3±0.2-7.8±1.9; Fig. 2) was comparatively more uniform than basal area within and among treatments.

When plants grew in isolation, total dry matter production at the end of the growing season was more than 79% greater ($p<0.05$) on defoliated and undefoliated plants of *S. ambigua* than in those of the other two species

(Table 1). Initial biomass, however, was the main determinant of this result because dry matter accumulated at the time of the first defoliation was more than 75% of total dry matter production on defoliated plants of the three species. In addition, tiller density was similar ($p>0.58$) in the three species [*S. ambigua* ($\bar{x}\pm1$ S.E.; n=2.8±0.2; 24), *S. tenuis* (2.4±0.2; 24), and *S. clarazii* (2.5±0.3; 24)] and the lower daughter tiller production was obtained on undefoliated parent tillers of *S. ambigua* (Table 2). A greater green+dry blade+stem+sheath length and height of undefoliated tillers in *S. ambigua* than in the other two species (Fig. 3) were comparatively more important than daughter tiller production and tiller density for explaining the observed response in total dry matter production. A greater ($p<0.05$) daughter tiller production (Table 2) and green+dry blade+stem+sheath length on undefoliated plants of *S. clarazii* grown in isolation (Fig. 3) determined a greater total dry matter production in this species than in *S. tenuis* (Table 1). Similar results were obtained when dry matter production was evaluated in the different neighborhood types and under different defoliation patterns. Dry matter production was greater ($P<0.05$) on the target *S. clarazii* than on its *S. tenuis*' neighbors for any defoliation treatment (Fig. 2). Production of dry matter was 53-131, 73-258 or 74-213% greater in *S. clarazii* than in *S. tenuis* when all plants remained undefoliated, only the target *S. clarazii* was defoliated or all plants were defoliated, respectively (Fig. 2). On the same way, *S. clarazii* and *S. tenuis*

Fig 3

had a similar ($P>0.07$) dry matter production when both species remained undefoliated in neighborhoods where *S. tenuis* was surrounded by *S. clarazii* (Fig. 2). However, dry matter production was greater ($P<0.05$) in *S. clarazii* than in *S. tenuis* when only the target *S. tenuis* or both species were defoliated (Fig. 2). These results suggest a greater competitive ability in *S. clarazii* than in *S. tenuis*, and that *S. clarazii* can take advantage of competition release after defoliation of *S. tenuis*; released soil resources may thus be utilized for increased growth in *S. clarazii*. These results are similar to those of Flemmer et al. (1997; 1998a) when both species grew distant 30 cm one from the other within a uniform matrix under rainfed, water stress or irrigated conditions.

A greater green+dry blade+stem+sheath length and height on undefoliated than on defoliated tillers of *S. ambigua* (Fig. 3) may have produced a greater shading of stem bases and a lower red/far red ratio. This may have contributed to the lower daughter tiller production on undefoliated than on defoliated tillers of the undesirable species (Table 2). The amount of light energy available has been mentioned as a major factor determining daughter tiller production in *Lolium perenne*: development of daughter tillers was inhibited as availability of light energy decreased (Mitchell 1953). Reductions in the red/far red ratio have also led to decreased production of new tillers in several perennial grasses (Casal et al. 1987, 1990; Skinner and Simmons 1993; Wan and Sosebee 1998).

However, increased red/far red ratios on undefoliated plants of *Schizachyrium scoparium* determined a similar new tiller production among plants where this ratio either was or was not enriched (Murphy and Briske 1994). The lack of consistent tillering responses between defoliated and undefoliated plants is due to the complexity of the physiological mechanisms regulating axillary bud growth and the large number of potentially intervening factors (e.g., environmental variables, species specific responses, stage of phenological development, and frequency and intensity of defoliation) (Murphy and Briske 1992; Briske and Richards 1995).

Plants of the three species which grew without nearby neighbors were defoliated once or twice during the growing season to evaluate their capacity for photosynthetic leaf area reestablishment after defoliation. Towards the end of the study, the amount of regrowth was greater in *S. clarazii* (0.058±0.034; 3) than in *S. tenuis* (0.023±0.010; 4) and *S. ambigua* (0.017±0.004; 4). Greater relative growth rates for green blades, stem+sheaths and blade+stem+sheaths, and height (Fig. 4), and a greater ($p<0.05$) daughter tiller production towards the end of the study (Table 2) in *S. clarazii* than in the other two species contributed to explain this response. These results suggest that *S. clarazii* is a superior competitor when compared to *S. tenuis* and *S. ambigua* since greater growth rates are positively related to competitive ability (Grime 1979). The more

Fig 4

competitive species also showed as the more tolerant to defoliation due to its greater daughter tiller production and tillers of fastest growth. A rapid photosynthetic canopy reestablishment through production of a greater number of daughter tillers of rapid growth has been reported to be essential in explaining grazing tolerance in several perennial tussock grasses (Caldwell et al. 1981; Briske and Richards 1995; Briske and Hendrickson 1998). Previous studies, however, had reported that *S. clarazii* is replaced by *S. tenuis* under moderate, continuous grazing (Distel and Bóo 1996).

Growth rates for green blade+stem+sheaths and height in all three species were greater on defoliated than on undefoliated tillers on plants which grew without nearby neighbors (Fig. 5). This most likely contributed to obtain a similar ($p>0.89$) total dry matter production in both defoliation treatments at the end of the study period (Table 1). Becker et al. (1997) also obtained a similar dry matter production on plants of *S. tenuis* which remained undefoliated or that were defoliated at different stages of internode elongation under natural conditions. Our results agree with those observed by A.C. Flemmer (unpublished work) 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. However, dry matter production was more than 26% lower on defoliated than on undefoliated plants of *S. clarazii* and *S. tenuis* when these species grew in competition with undefoliated *S. gynerioides* under irrigation (A.C. Flemmer, unpublished work). Under these latter conditions of water availability, greater biomass of *S. gynerioides* determined that photosynthetically active radiation to stem bases height in *S. clarazii* and *S. tenuis* was on average 74% lower than in the rainfed or water stress treatment (Flemmer et al. 1998b). 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. However, growth of defoliated *S. clarazii* was not inhibited by undefoliated neighbors of *S. tenuis* or *S. ambigua* in our study (Fig. 2). Aboveground biomass of these latter species very likely did not prevent light from reaching the stem bases of the target, defoliated *S. clarazii*.

Dry matter production was greater (P<0.05) on defoliated than on undefoliated plants of *S. clarazii* (Fig. 2). This emphasizes that this species can rapidly reestablish photosynthetic tissues after defoliation and is tolerant to this biotic stress. Plants tolerant to defoliation exhibit a high meristematic activity and specific physiological processes, such as a greater relative allocation of carbon to aboveground sinks, which contribute to its increased rate of photosynthetic canopy reestablishment (Briske and Richards 1994, 1995). *Stipa clarazii* thus showed a greater dry matter production when compared to the other two species whether it grew in isolation or surrounded by nearby neighbors. This again highlights *S.*

clarazii as a superior competitor, in agreement with results of Moretto (1998). Anderson and Briske (1995) reported similar results in *Schizachyrium scoparium*: late-seral species can have an either similar or greater tolerance to defoliation than earlier-seral species. As it was reported for *S. scoparium*, selective herbivory of *S. clarazii*, rather than its tolerance to defoliation, would be the major factor driving its replacement by undesirable perennial grasses in rangelands of Central Argentina. Moretto and Distel (1997) and Moretto (1998) arrived to a similar conclusion in this species. The influence of selective herbivory on the intensity and duration of competitive interactions, however, could be minimized under conditions of a low and 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, a continuous defoliation could reduce sexual reproduction in some species thereby affecting plant demography and community composition (O'Connor 1991).

Dry matter production was lower ($P<0.01$) in *S. tenuis* whenever this species was surrounded by neighbors of *S. ambigua* (Fig. 2). Growth rates were 0.0001 gr dry weight cm^{-2} d^{-1} in *S. tenuis* and more than 3 times this value for all *S. ambigua* neighbors (data not shown). The undesirable *S. ambigua* showed then characteristics of a species more tolerant to defoliation than *S. tenuis*. Defoliated and undefoliated plants of *S. ambigua* had a similar (*P*>0.19) dry matter production when in competition with plants of *S. tenuis* (Fig. 2). Even more, dry matter production was greater (*P*<0.05) on defoliated than on undefoliated plants of *S. ambigua* whenever the target species was *S. clarazii* (Fig. 2). Previous studies, however, suggested that tolerance to defoliation would likely be lower on undesirable (e.g., *S. gynerioides*) than on desirable (e.g., *S. tenuis*) perennial tussock grasses (Bóo et al. 1996). Results obtained for *S. ambigua* in our study are conspicuous in a species which owes its grazing resistance mainly to avoidance mechanisms. This species is only cut off when a better forage is not available (Cano 1988). Low palatability in *S. ambigua* could partially be explained by its high lignin ($\bar{x}$=9.4%) and low crude protein ($\bar{x}$=8.9%) contents in comparison to values observed in the palatable species *S. clarazii* ($\bar{x}$=5.5% for lignin and 13.7% for crude protein) (H.D. Giorgetti, O.A. Montenegro and G.D. Rodríguez, unpublished data). A negative correlation between production of secondary compounds and leaf growth is often assumed (e.g., Skogsmyr and Fagerstrom 1992; Loehle 1996). Such a response between avoidance mechanisms and competitive ability, however, were not evident in the undesirable *S. ambigua*. A species may have a competitive advantage in the community if it is defoliated less intensively (avoidance mechanisms), is able to sustain rapid regrowth after defoliation (tolerance mechanisms) or possess a combination of both grazing resistance mechanisms (Briske 1991). In addition, greater growth on any given species may have implications in its capacity for soil resource acquisition. For example, when two perennial grass species (*S. scoparium* and *Paspalum plicatulum*) grew one near the 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).

Stipa tenuis appeared to be the less tolerant species to defoliation in all neighborhoods studied. However, its response differed when plants were grown without nearby neighbors. Under these conditions, the similar regrowth production in *S. tenuis* and *S. ambigua* suggests that the desirable species is able to utilize soil resources when they are available and produce a greater growth in absence of nearby competitors. Plant biomass removal within a 2m-radius around individual plants of *Schizachyrium scoparium* increased biomass in this species from 3 to 8 times; neighboring plants had been reducing levels of available ammonium+nitrate from 3 to 9 times (Tilman 1989).

This study demonstrated that later-seral species may or may not show a greater competitive ability or tolerance to defoliation than earlier-seral species. Proximity of nearby neighbors appeared to be a major determinant of the obtained response. Both competitive ability and tolerance to defoliation were always greater in *S. clarazii* than in *S. tenuis* and *S. ambigua*, independently of neighbor proximity. However, even though *S. tenuis* showed a lower competitive ability and tolerance to defoliation than *S. ambigua* when the desirable species had nearby neighbors of the undesirable one, both attributes were similar for both species when they grew in isolation. Defoliation treatment characteristics in any study should repeat over seasons or years to induce unequivocal plant responses (Briske and Hendrickson 1998). Long-term studies should then be a focus of future research to corroborate results obtained in our investigation.

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Table legends

Table 1 Total dry matter production on plants of *S. clarazii*, *S. tenuis* and *S. ambigua* which were either defoliated or not during the 1998 study period. Each value is the average ($\bar{x}$)± 1 standard error (SE) of n=3-4 plants

Table 2 Number of daughters on parent tillers of *S. clarazii*, *S. tenuis* and *S. ambigua* which were either defoliated or not during the 1998 study period. Values are $\bar{x}$ ±1 SE of n=12-16 tillers, and correspond to the last sampling date on 4 December.

Figure legends

Fig. 1 **(a)** Absolute monthly maximum and minimum, and mean monthly air temperatures, **(b)** mean monthly soil temperatures at 0.05, 0.10 and 0.50 m depth, **(c)** absolute monthly maximum and minimum, and mean monthly relative humidities, **(d)** mean monthly wind speed and saturation water vapour deficit, and **(e)** mean monthly pan evaporation and monthly rainfall during 1998 at a meteorological station located at the study site

Fig. 2 Tiller density (number/cm^2), and total dry matter production on a tiller or surface area basis on plants of *S. clarazii*, *S. tenuis* and *S. ambigua* exposed to different defoliation patterns (Control=all plants remained undefoliated, only the target was defoliated or both target and neighbors were defoliated) under various neighborhood types (indicated at the top of panels). Target refers to an individual of any species surrounded by neighbors of another species. Neighbor 1 is always the closest to the target. Each histogram is the $\bar{x} \pm 1$ SE of $n=6$

Fig. 3 Green+dry blade+stem+sheath length and height on tillers of *S. clarazii*, *S. tenuis* and *S. ambigua* plants which remained undefoliated during the 1998 study period. Each symbol is the $\bar{x}$ of $n=14$-48 tillers. Vertical bars indicate ± an average of the SE of the means

Fig. 4 Relative growth rates for blade, stem+sheath or blade+stem+sheath length, and height on defoliated tillers of *S. clarazii*, *S. tenuis* and *S. ambigua* plants during 9 November to 4 December 1998. Each histogram is the x̄±1 SE of n=4 plants

Fig. 5 Growth rates for green blade+stem+sheath length and height on tillers of *S. clarazii*, *S. tenuis* and *S. ambigua* plants which were either defoliated or not during the 1998 study period. Periods utilized to calculate such rates are given in the abscissa. Each histogram is the x̄±1 SE of n=4-8 plants

Table 1

Total dry matter (g/cm^2)		
	Defoliated plants	Undefoliated plants
S. tenuis	0.059±0.02 a*	0.051±0.02 a
S. clarazii	0.174±0.02 b	0.125±0.05 b
S. ambigua	0.310±0.02 c	0.274±0.07 c

* Values are means ± SE (n=4). Means within columns followed by a different letter are statistically different ($p<0.05$).

Table 2

	Number of daughters per parent tiller	
	Defoliated plants	Undefoliated plants
S. tenuis	0.94±0.29 a*	0.62±0.24 a
S. clarazii	1.75±0.41 a	2.25±0.28 b
S. ambigua	1.31±0.38 a	0.44±0.22 a

* Values are means ± SE. Means within column followed by a different letter are statistically different ($p<0.05$).

10P

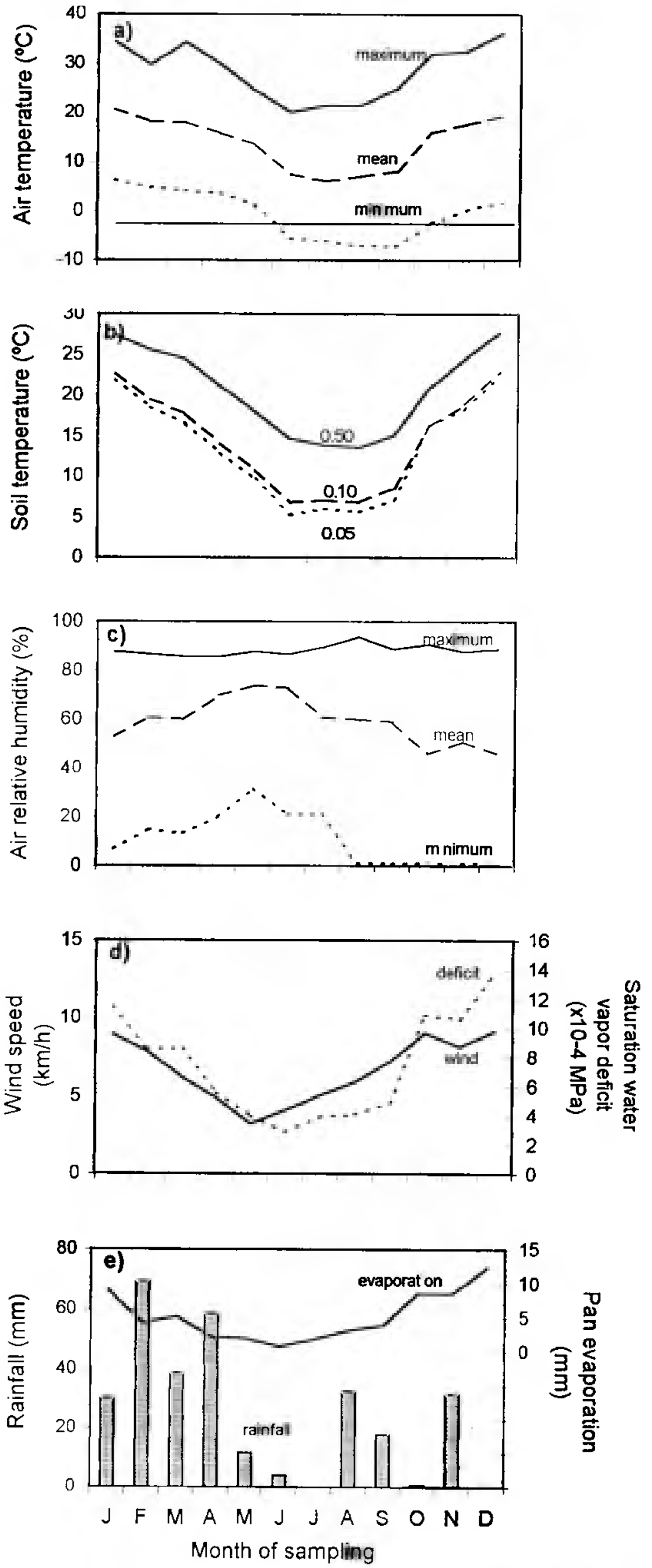

Fig 1 – Saint Pierre, Busso, Montenegro, Rodríguez, Giorgetti, Montani, [illegible]

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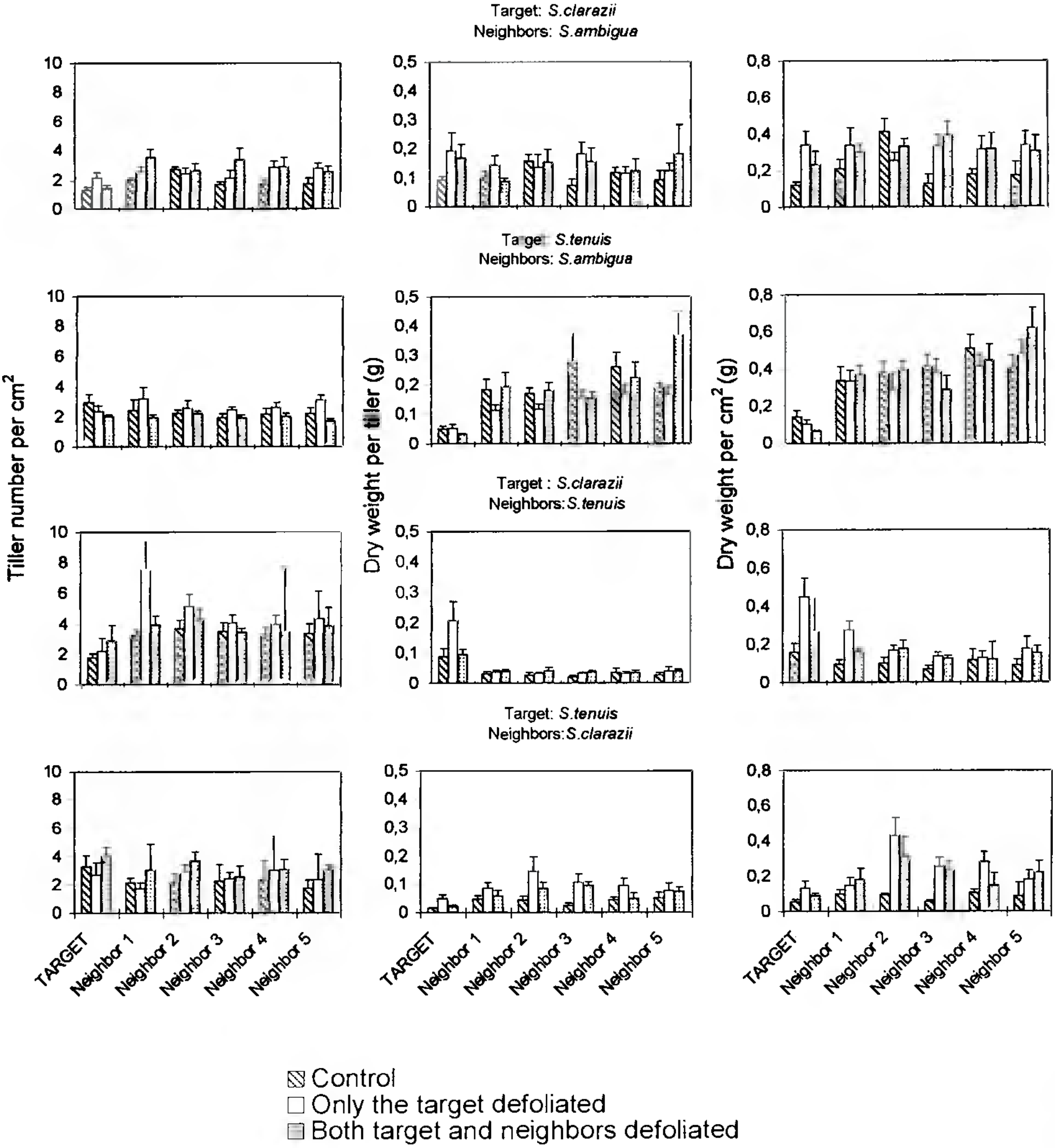

Fig 2. - Saint Pierre, Busso, Montenegro, Rodriguez, Giorgetti, Mon[illegible] [illegible]

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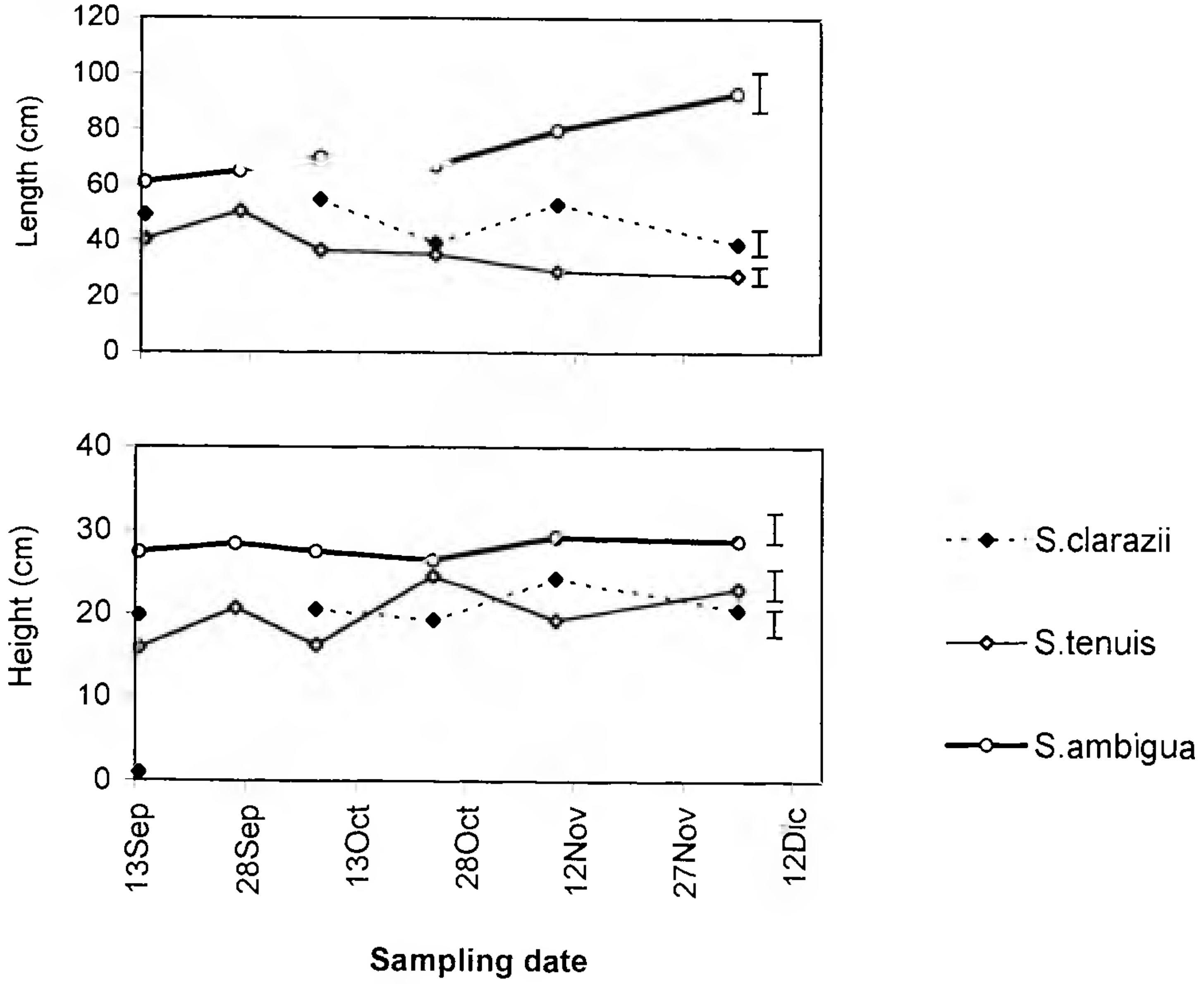
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80
60
40
20
0
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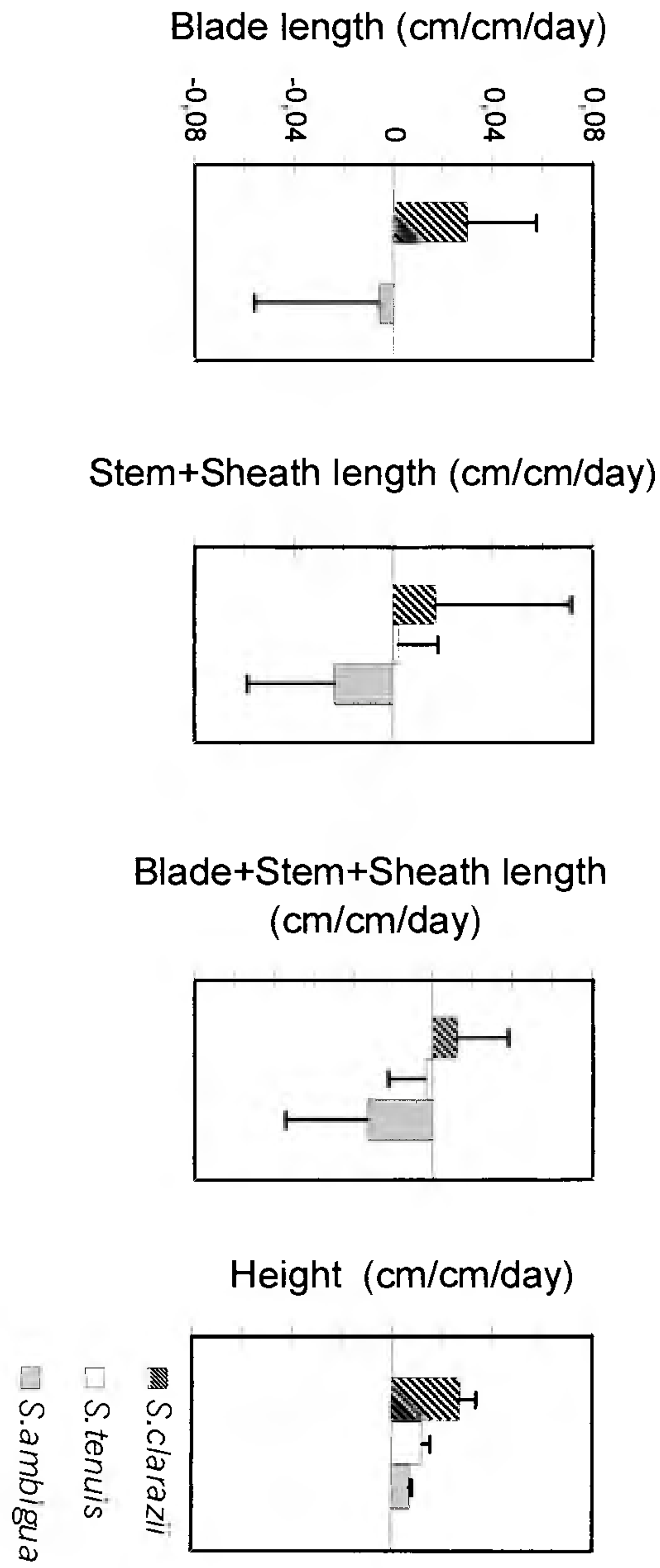
40
30
20
10
0
Height (cm)
13Sep
28Sep
13Oct
28Oct
12Nov
27Nov
12Dic
Sampling date
S.clarazii
S.tenuis
S.ambigua

Fig 3 - [illegible]

Fig 4



Blade length (cm/cm/day)

Stem+Sheath length (cm/cm/day)

Blade+Stem+Sheath length (cm/cm/day)

Height (cm/cm/day)

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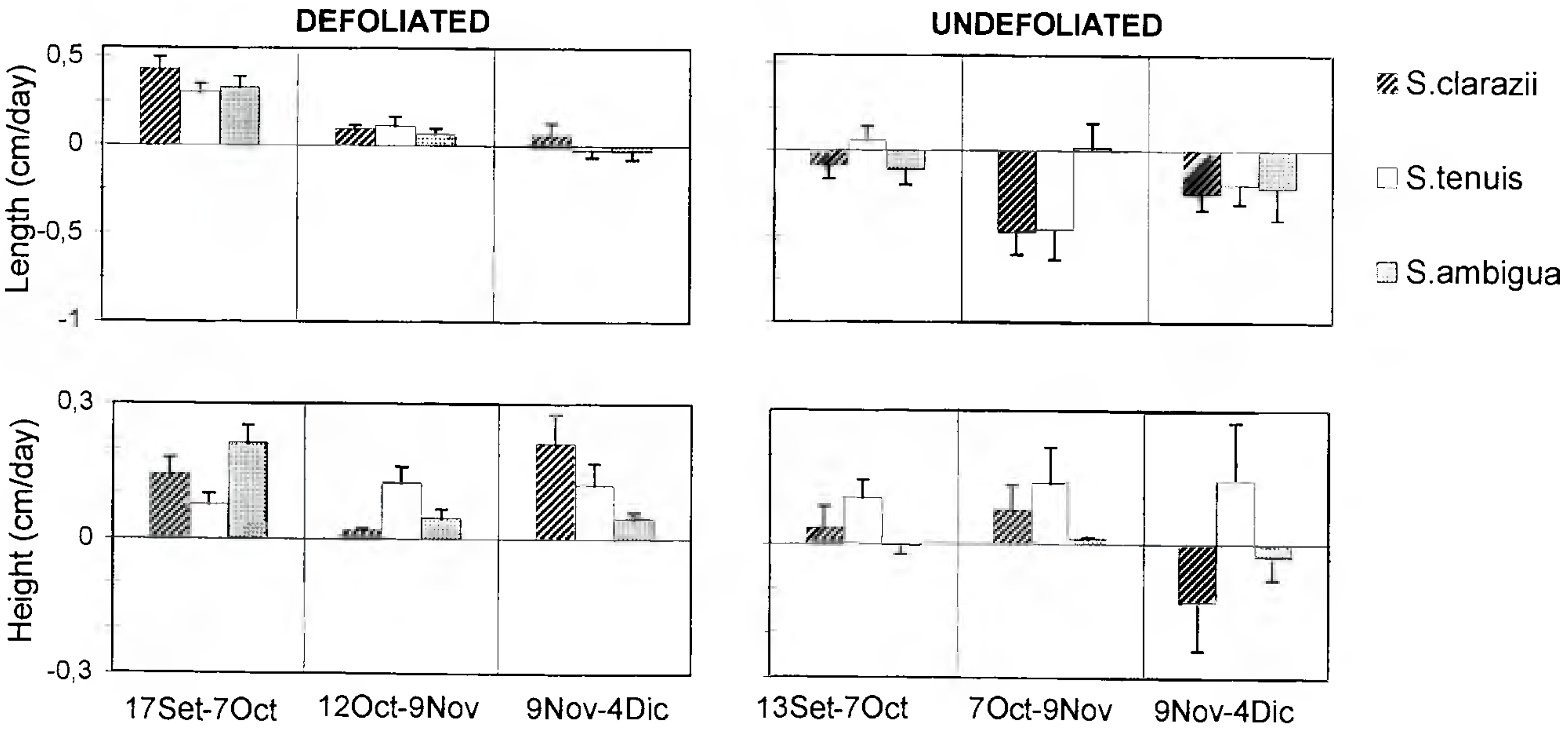

Fig 5 - Saint Pierre, Busso, Montenegro, Rodriguez, Giorgetti, [illegible], [illegible]