Influence of woody species on aerial growth of perennial grasses in semi-arid rangelands of central Argentina

Influencia de especies leñosas en el crecimiento aéreo de gramíneas perennes en pastizales semiáridos del centro de Argentina

Blazquez FR[1,2,3], DV Peláez[1,3,4], RJ Andrioli[1], OR Elia[1,2,3]

Abstract. The interaction between woody and grass species in semi-arid rangelands of central Argentina was assessed through the evaluation of the impact of woody species on grass growth over a 2-y period. The study comprised two morpho-physiologically different woody species and two cool-season perennial grass species highly preferred by domestic livestock. The study involved the assessment of total green length (TGL) and number of green leaves (NGL) per tiller in grasses growing beneath the canopy of woody species and in open rangeland areas. Soil temperature, pH and water, nitrogen, phosphorus and organic matter content were estimated at the same study sites. Precipitation during the study period was also recorded. Woody species induced higher TGL of grasses growing beneath their canopy when rainfall was near or above the long-term average for the study site and had no effect on NGL. Nitrogen and organic matter content of soils beneath the canopy of woody species were higher than values in open areas, while differences in the other soil parameters were scarce. Overall, the results of the present study suggest that woody species exert a facilitative effect on perennial grass species in semi-arid rangelands of central Argentina.

Keywords: Canopy architecture; Soil temperature; Soil water content; Tiller green length.

Resumen. La interacción entre especies leñosas y gramíneas en pastizales semiáridos del centro de Argentina fue evaluada a través del impacto de las especies leñosas sobre el crecimiento de las gramíneas durante un período de dos años. El estudio involucró a dos especies leñosas de diferentes características morfo-fisiológicas y a dos gramíneas perennes de ciclo otoño-inverno-primaveral altamente preferidas por el ganado doméstico. Se determinó la longitud total verde (LTV) y número de verdes hojas (NHV) por macolla en plantas de las gramíneas creciendo bajo la canopia de las especies leñosas y en sitios abiertos del pastizal; mientras que, la temperatura del suelo, pH y contenido de agua, nitrógeno, fósforo y materia orgánica se estimaron en los mismos sitios. También se registró la precipitación durante el período de estudio. Las gramíneas que crecieron bajo la canopia de las especies leñosas tuvieron mayor LTV cuando la precipitación fue similar o superior al promedio histórico del sitio de estudio; sin embargo, no se detectaron diferencias en el NHV. El contenido de nitrógeno y de materia orgánica en el suelo debajo de la canopia de las especies leñosas fue mayor que en los sitios abiertos; mientras que, las diferencias en los otros parámetros del suelo fueron escasas y las posibles causas de ello son discutidas. En general, los resultados del presente estudio sugieren que las especies leñosas ejercen un efecto facilitador sobre las gramíneas perennes en los pastizales semiáridos del centro de Argentina.

Palabras clave: Arquitectura de la canopia; Temperatura del suelo; Contenido de agua del suelo; Longitud verde de la macollas.

[1] Departamento de Agronomía, Universidad Nacional del Sur, 8000 Bahía Blanca, Argentina.
[2] Consejo de Investigaciones Científicas y Técnicas (CONICET), Argentina.
[3] Centro de Recursos Naturales Renovables de la Zona Semiárida (CERZOS), Argentina.
[4] Comisión de Investigaciones Científicas de la Provincia de Buenos Aires (CIC), Argentina.
Address Correspondence to: Francisco R. Blazquez, *e-mail:* francisco.blazquez@uns.edu.ar

INTRODUCTION

Grasslands, shrublands, savannas, forests and drylands, which can be collectively addressed as rangelands, occupy about 45-52% of the Earth's surface (Matthews, 1983). Plant communities in these ecosystems are typically formed by a continuous layer of grass species and a discontinuous one of woody species. The influence of herbivory, fire, soil and climate on both vegetation layers have been thoroughly studied (Sala, 1988; McNaughton, 1991). However, the understanding of the interactions between woody and perennial grass species in semi-arid ecosystems still remains elusive.

The coexistence of woody and perennial grass species in semi-arid ecosystems has been attributed to the combined effect of water and nutrient availability, fire frequency and intensity, and herbivory (Werner, 1990). The structure of the community is shaped by the interaction among these biotic and abiotic factors, and the complex balance of competitive and facilitative mechanisms that operate simultaneously between neighbouring species (Callaway & Walker 1997).

It has been proposed, through the 'stress-gradient hypothesis' (SGH), that the relative frequency of competitive and facilitative mechanisms varies inversely across abiotic stress gradients (Bertness & Callaway, 1994). According to this hypothesis, facilitation is more common under stressful abiotic conditions, even though it may decrease or cease under extreme stress, while competition prevails under more favourable abiotic conditions. It has also been suggested that the balance between these mechanisms depends, to a large extent, on the characteristics of the species involved in the interaction (Choler et al., 2001).

The aftermath of the interaction between woody and perennial grass species has been assessed by comparing the grass species productivity at sites located under the canopy of woody species individuals with that in open rangeland areas. Several mechanisms have been identified as responsible for the differences found in grass productivity between sites. Competition for light, water and nutrients has been the major recognized mechanism (Walter, 1971; Walker & Noy-Meir, 1982; McMurtrie & Wolf, 1983; Scholes & Archer, 1997). Thereafter, the most common facilitative mechanisms identified have been the (1) increase in soil nutrient content and structure beneath the canopy of woody species, accounted for by litter inputs from the woody species (Whitford et al., 1996; Weltzen & Coughenour, 1990), and (2) amelioration of grass water status, through a reduction in the amount of incident solar radiation which translates into lower temperatures and, ultimately, into reduced evapotranspiration beneath the woody species canopy (Ludwig et al., 2004).

In semi-arid rangelands of the southern Caldenal (Cabrera, 1976), located in central Argentina, land is almost exclusively used for cattle raising. Long-term overgrazing and the lengthening of the fire-free period have induced changes in the structure of plant communities. This has been through an increase in abundance of woody species and a decrease in the abundance and productivity of perennial grass species (Distel & Bóo, 1996). Woody species control and management strategies aimed to restore the grassland productivity have been elaborated. However, the extent to which woody species should be removed, in terms of rangeland sustainability, is yet unknown. Hence, studies attempting to elucidate the effect of woody species on growth of perennial grass species in this region are needed.

The specific objective of this study was to evaluate the effect of two morpho-physiologically different woody species on growth of two cool-season perennial grass species highly preferred by domestic livestock in the southern Caldenal. This was achieved after assessing of the impact of those woody species on grass and soil parameters that are major determinants of grass growth.

MATERIALS AND METHODS

Study site. This study was conducted at a representative site of the Caldenal, located in the south-eastern corner of the province of La Pampa in central Argentina (38° 45' S, 63° 45' W). The leveled, 20-ha study site was (1) located within a pasture with no recent fire history and (2) fenced since 1982 to exclude livestock grazing.

The climate of the region is temperate and semiarid (Instituto Nacional de Tecnología Agropecuaria, 1980). Mean monthly air temperatures range from a low of 7 °C in July to a high of 24 °C in January, with an annual mean of 15 °C. Mean annual rainfall is 400 mm, highly variable between years and with peaks in autumn and spring. Mean annual potential evapotranspiration is 800 mm. Annual precipitation during the study period was 369 mm in 2011 and 510 mm in 2012 (Servicio Meteorológico Nacional, 2013). Its distribution was approximately similar to that of the long-term average (40-y), except for deeper water deficits in summer and winter, and the higher rainfall records in spring (Fig. 1). Soils are medium to coarse-textured Calciustolls (Sánchez & Lazzari, 1999), with a petrocalcic horizon commonly found at 60–80 cm depth.

The physiognomy of the vegetation is grassland with scattered woody plants (Distel & Bóo, 1996). The herbaceous layer is dominated by perennial cool-season grasses such as *Piptochaetium napostaense* (Speg.) Hack., *Nassella tenuis* (Phil.) Bark., *Nassella clarazii* (Ball) Bark. and *Poa ligularis* Ness ex Steud. Other common grasses at the study site include *Jarava ichu* (Ruiz et Pav.) and *Pappostipa speciosa* (Trin et Rupr.) Rom. The shrub layer is constituted by warm-season deciduous species and evergreen species. The former is mainly represented by *Prosopis caldenia* and *Prosopis flexuosa* DC., and the latter by *Larrea divaricata*, *Condalia microphylla* Cav., and *Chuquiraga erinacea* D. Don (Bóo & Peláez, 1991; Distel & Peláez, 1985).
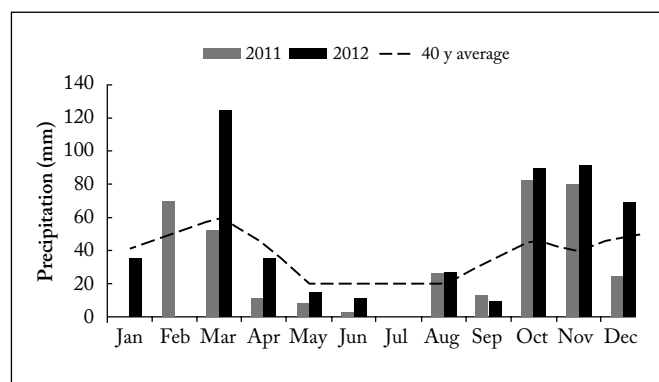
Experimental design. The species chosen for the study were *P. caldenia* and *L. divaricata*, a warm-season deciduous and an evergreen woody species, respectively; and *N. clarazii* and *P. napostaense* as representatives of perennial grasses highly preferred by livestock (Bontti et al., 1999; Bóo et al., 1993; Pisani et al., 2000). Six plants of each woody species were randomly selected at the study site. An individual of each grass species was chosen both beneath the canopy of each woody species individual and in the open area (~2 m away from the shrub crown). Six tillers were labelled in each grass plant (3 in the centre and 3 in the outer boundary of the crown) using coloured wire rings.

Aerial growth measurements. Two morphogenetic traits were measured on each tiller in order to assess the aerial growth of grasses; namely the total green length (TGL), and the number of green leaves (NGL). Measurements were made periodically during two growing seasons (May-Dec 2011 and March-Dec 2012) with an increasing frequency towards the end of the growth cycle (i.e., from 30 to 15-d interval between measurements). At the beginning of each growth cycle plants were defoliated to almost ground level (4 cm). Afterwards, on each tiller, the TGL was calculated as the sum of the following measurements made using a 1-mm graduated ruler: (*i*) green blade length, measured from the tip of fully expanded leaves to their own ligule, or from the tip of growing leaves to the ligule of the previously fully expanded leaf, (*ii*) pseudostem measured from the soil to the ligule of the last fully expanded leaf, and (*iii*) true stem measured from the ligule of the flag leaf to the base of the panicle. The NGL was recorded on each date by counting the number of growing or fully expanded leaves that did not have signs of senescence.

Soil sampling. At the time of each aerial growth measurement, soil temperature (5 cm deep) was recorded by using thermocouples type E (chromel-constantan) connected to a microvoltmeter (HR-33T, Wescor Inc., Logan, UT, USA). Measurements were made both beneath the canopy and in the open area (~2 m away from the shrub crown) of each woody species individual.

Simultaneously, in 2011, one soil core (3 cm diameter x 20 cm deep) was collected beneath the canopy of each woody species while another six soil cores were taken in the open area (>2 m away from any woody species canopy). Samples were taken to the laboratory to determine soil gravimetric water content. In 2012, the soil sampling procedure was modified as follows: one soil core was taken beneath the canopy, while another one was taken in the open area (~2 m away from the shrub crown) of each woody species individual.

Additionally, at the end of the woody species growth cycle (March 2012), soil samples were analysed for nitrogen (semi-micro Kjeldahl procedure; Bremner & Mulvaney, 1982), phosphorus (extractable P; Bray and Kurtz 1945); organic matter (wet oxidation; Walkley-Black 1934) and pH.

Statistical analyses. Data were analysed as a split-split plot design with (1) woody species individuals as plots, (2) locations (beneath canopy *vs.* open area) as subplots, and (3) sampling date as sub-subplot for each grass species and year separately. The model effects were woody species, location and perennial grass species. Data of TGL were log-transformed to meet normality and homocedasticity. Means were compared by Tukey HSD test (Snedecor & Cochran, 1980) when significant differences were found. All statistical analyses were performed with JMP 7.0 (SAS Institute 2007).

RESULTS

Overall, the TGL and NGL of both grass species varied across time both within each year and between years ($p<0.05$). Both growth parameters showed their lowest values ($p<0.05$) during autumn and winter in 2011 and 2012, and increased significantly in spring (Fig. 2 and 3). There was no significant effect of location on the NGL ($p<0.05$). However, the TGL of grasses was higher beneath the canopy of the woody species than in the open areas during spring 2011 for *N. clarazii*, and at most of the sampling dates in 2012 for both grass species (Fig. 2). Generally, there was no significant effect of the woody species on TGL or NGL. The only exceptions were *N. clarazii* for TGL in late spring 2011, and both grass species in late spring 2012: TGL of grass plants located beneath the canopy of *P. caldenia* was higher than that beneath the canopy of *L. divaricata* ($p<0.05$) (Fig. 2).

Soil temperature was similar ($p>0.05$) among woody species and location during autumn and winter both in 2011 and 2012. Differences in soil temperature were mostly apparent in spring in both years (Table 1). At this time, soil temperature was lower ($p<0.05$) beneath the canopy of *P. caldenia* than in
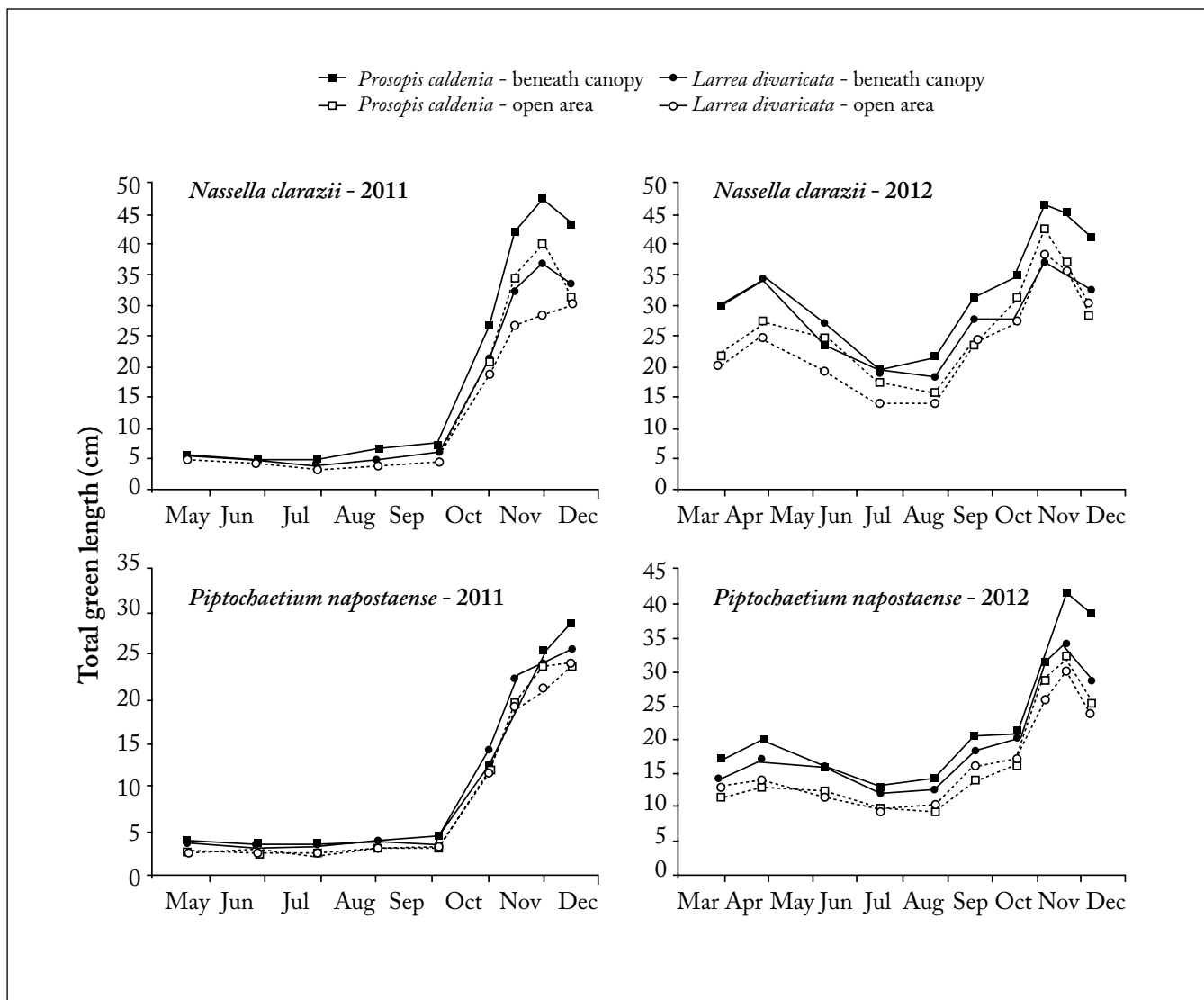
Fig. 2. Mean total green length (TGL) on tillers of *N. clarazii* and *P. napostaense* beneath the canopy and in open areas (~2 m away from the crown) of *P. caldenia* and *L. divaricata* in 2011 and 2012. Values are means of 6 replicates. Note graphic scale change in y axis for P. napostaense in 2011 and 2012.

Fig. 2. Longitud total verde media (TGL) en macollas de *N. clarazi*i y *P. napostaense* debajo de la canopia y en áreas abiertas (~2 m alejadas de la corona) de *L. caldenia* y *L. divaricata* en 2011 y 2012. Los valores son las medias de 6 réplicas. Notar los cambios de escala en eje y para P. napostaense en 2011 y 2012.

the open areas at most of the sampling dates both in 2011 and 2012; however, there were no differences (p>0.05) between locations in *L. divaricata* (Table 1).

Soil water content was similar (p>0.05) among woody species and location throughout 2011 (Table 2). The only exception occurred at the last sampling date, when soil water content was significantly lower beneath the canopy of *P. caldenia* than beneath that of *L. divaricata* (Table 2). In 2012, there was no significant (p>0.05) effect of location on soil water

content. The only exception was *L. divaricata* (p<0.05) at the first sampling date. However, there were significant differences (p<0.05) in soil water content between woody species at four sampling dates (Table 2).

Soil N and OM content significantly differed (p<0.05) between locations regardless of woody species, values were higher beneath each woody species canopy than in the open areas (Table 3). On the other hand, there were no significant differences in P content or pH (p>0.05).
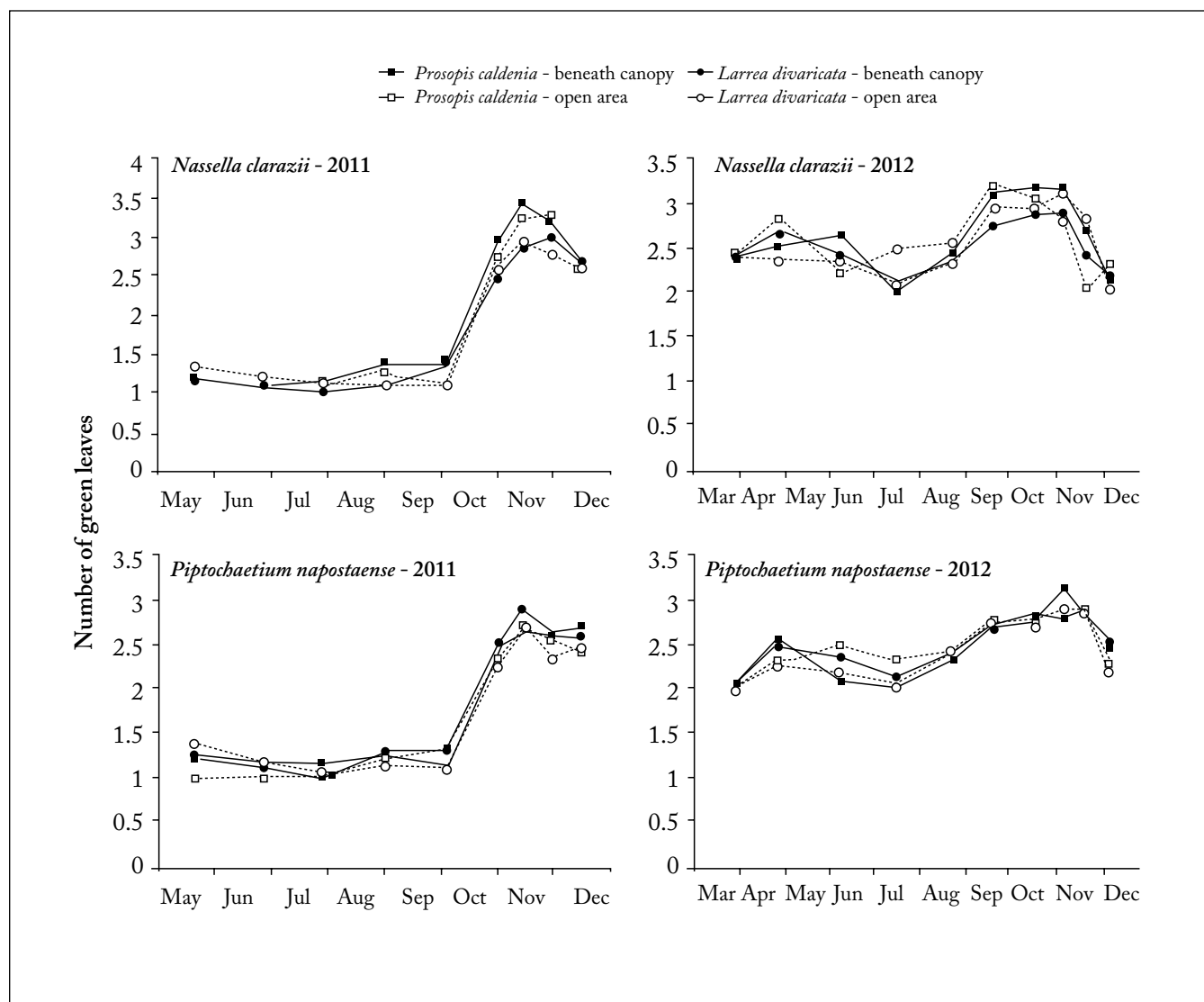
Fig. 3. Mean number of green leaves (NGL) on tillers of *N. clarazii* and *P. napostaense* beneath the canopy and in open areas (~2 m away from the crown) of *P. caldenia* and *L. divaricata* in 2011 and 2012. Values are means of 6 replicates. Note graphic scale change in y axis for N. clarazii in 2011 and 2012.

Fig. 3. Número de hojas verdes media en macollas de *N. clarazii* y *P. napostaense* debajo de la canopia y en áreas abiertas (~2 m alejadas de la corona) de *P. caldenia* y *L. divaricata* en 2011 y 2012. Los valores son las medias de 6 réplicas. Notar los cambios de escala en eje y para N. clarazii en 2011 y 2012.

DISCUSSION

Overall, woody species effect on grass TGL was neutral in 2011 while positive in 2012. This difference was probably accounted for by differences in precipitation between years. Accordingly, in 2011, there were no significant differences in TGL between *N. clarazii* and *P. napostaense* both beneath the canopy of the woody species and in the open areas during autumn and winter (from May to September). TGL of both grass species

was low (less than 5 cm) during that period (Fig. 2), when rainfall records were below the long-term average (Fig. 1). From this time onwards, however, rainfall was above the long-term average until the end of this growth cycle. This may have allowed both grass species to resume growth immediately. Together with the onset of flowering, this might help explain the increase in TGL towards the end of the growth period. This is because during the reproductive phase, grass internodes elongate protruding first the leaves that were formerly within the pseudostem, and immediately afterwards, the panicle (Langer,

Table 1. Soil temperature at 5 cm soil depth beneath the canopy and in the open areas (~2 m away from the crown) of *P. caldenia* and *L. divaricata* in 2011 and 2012. Values are means of 6 replicates; SEM equalled 0.8 both in 2011 and 2012. Within each year and column, values followed by the same letter are not significantly different (p>0.05).
Tabla 1. Temperatura del suelo a 5 cm de profundidad debajo de la canopia y en áreas abiertas (~2 m alejadas de la corona) de *P. caldenia* y *L. divaricata* en 2011 y 2012. Los valores son las medias de 6 réplicas; ESM igual a 0,8 en 2011 y 2012). Dentro de cada año y columna, valores seguidos de la misma letra no son significativamente diferentes (p>0,05).

Soil temperature (°C)										
2011		May 20	Jun 27	Jul 29	Sep 1	Oct 4	Nov 1	Nov 15	Nov 30	Dec 16
P. caldenia	beneath canopy	13.1 a	3.3 a	8.9 a	9.5 a	14.1 a	17.8 a	17.8 a	17.0 c	21.4 c
	open area	12.7 a	2.5 b	8.9 a	9.5 a	15.1 a	21.7 a	21.7 a	22.7 a	28.3 a
L. divaricata	beneath canopy	13.1 a	3.2 ab	9.3 a	10.0 a	15.6 a	19.5 a	19.5 a	18.6 bc	23.9 bc
	open area	12.8 a	2.6 b	8.6 a	9.5 a	14.5 a	18.3 a	18.3 a	19.9 b	25.4 ab
2012		Mar 29	Apr 27	Jun 8	Jul 16	Sep 19	Oct 18	Nov 6	Nov 21	Dec 7
P. caldenia	beneath canopy	14.1 a	9.7 a	0.8 a	4.4 a	11.6 b	15.6 a	19.3 c	21.4 c	17.8 c
	open area	17.8 a	10.4 a	1.4 a	4.7 a	15.6 a	16.8 a	23.8 a	27.5 a	23.0 a
L. divaricata	beneath canopy	14.5 a	9.8 a	0.9 a	5.0 a	13.2 ab	15.7 a	20.5 bc	23.1 bc	19.4 bc
	open area	14.5 a	9.6 a	0.4 a	4.6 a	15.7 a	15.8 a	21.9 ab	24.8 ab	21.5 ab

Table 2. Soil gravimetric water content at 0-20 cm soil depth beneath the canopy versus open areas (~2 m away from the crown) of *P. caldenia* and *L. divaricata* in 2011 and 2012. Values are means of 6 replicates, SEM equalled 0.6 in 2011 and 0.7 in 2012. Within each year and column, values followed by the same letter are not significantly different (p>0.05).
Tabla 2. Humedad gravimétrica del suelo a 0-20 cm de profundidad debajo de la canopia y en áreas abiertas (~2 m alejadas de la corona) de *P. caldenia* y *L. divaricata* en 2011 y 2012. Los valores son las medias de 6 réplicas; ESM igual a 0,6 en 2011 y 0,7 en 2012). Dentro de cada año y columna, valores seguidos de la misma letra no son significativamente diferentes (p>0,05).

Soil gravimetric water content (%)										
2011		May 20	Jun 27	Jul 29	Sep 1	Oct 4	Nov 1	Nov 15	Nov 30	Dec 16
P. caldenia	beneath canopy	7.65 a	7.1 a	7.65 a	9.28 a	6.72 a	9.8 a	9.67 a	11.24 a	7.06 a
L. divaricata	beneath canopy	7.52 a	7.34 a	7.76 a	9.22 a	5.78 a	8.67 a	10.87 a	11.2 a	10.12 b
	open area	7.87 a	7.65 a	7.97 a	9.73 a	5.3 a	7.46 a	8.45 a	11.89 a	8.41 ab
2012		Mar 29	Apr 27	Jun 8	Jul 16	Aug 23	Sep 19	Oct 18	Nov 6	Nov 21	Dec 7
P. caldenia	beneath canopy	12.5 ab	11.2 ab	12.6 a	10.0 a	15.6 b	10.2	22.2 a	9.2 a	7.6 a	14.3 a
	open area	12.6 ab	11.7 a	13.0 a	9.4 a	15.9 ab	10.3	21.8 a	8.9 ab	6.3 a	14.5 a
L. divaricata	beneath canopy	13.9 a	10.0 b	12.0 a	8.3 a	17.1 ab	10.2	20.8 ab	7.2 bc	6.7 a	16.7 a
	open area	11.7 b	10.0 b	12.0 a	8.6 a	17.3 a	10.0	19.6 b	7.0 c	5.5 a	15.7 a

Table 3. Soil nitrogen, phosphorus, organic matter content and pH at 0-20 cm soil depth beneath the canopy *versus* open areas (~2 m away from the crown) of *P. caldenia* and *L. divaricata* in March 2012. Values are means of 6 replicates ± SD. Within each column, values followed by the same letter are not significantly different (p>0.05).
Table 3. Contenido de nitrógeno, fósforo y contenido de materia orgánica en el suelo y pH a 0-20 cm debajo de la canopia y en áreas abiertas (~2 m alejadas de la corona) de *P. caldenia* y *L. divaricata* en Marzo 2012. Los valores son las medias de 6 réplicas ± DS. Dentro de cada columna, valores seguidos de la misma letra no son significativamente diferentes (p>0,05).

		N (%)	P (ppm)	OM (%)	pH
P. caldenia	beneath canopy	0.13 ± 0.02 a	6.86 ± 1.67 a	2.23 ± 0.42 a	8.08 ± 0.17 a
	open area	0.1 ± 0.02 bc	6.91 ± 1.45 a	1.64 ± 0.46 bc	8.12 ± 0.16 a
L. divaricata	beneath canopy	0.12 ± 0.01 ab	7.51 ± 2.24 a	1.97 ± 0.41 ab	7.78 ± 0.46 a
	open area	0.09 ± 0.01 c	6.27 ± 2.15 a	1.47 ± 0.22 c	8.09 ± 0.58 a

1972). These leaves, as well as the peduncle of the panicle, added up to the TGL and would account for the marked increase of this parameter in spring. Notwithstanding these differences in TGL across time, differences between locations in spring (from October to December) were only found in *N. clarazii* for both study woody species (Fig. 2). This might be attributed to species-specific characteristics: it has been shown that *N. clarazii* has a higher competitive ability than *P. napostaense* (Saint Pierre & Busso, 2006). Thereafter, a higher resource acquisition ability might explain the faster response to increased water availability in *N. clarazii* than in *P. napostaense* (Fig. 2).

In 2012, TGL in *N. clarazii* and *P. napostaense* was higher beneath the canopy of either *P. caldenia* or *L. divaricata* than in the open areas throughout the growth cycle (Fig. 2); this is in agreement with near- or above-average monthly rainfall records (Fig. 1). The differences in TGL between locations cannot be attributed to differences in soil water content since these were scarce (Table 2). They rather might be explained by differences in soil N and OM content, since these parameters where higher beneath woody species than in open areas (Table 3). Similar results were reported by Belsky et al. (1989) for *Acacia tortilis* and *Adansonia digitata* in African savannas, and by López-Pintor et al. (2006) for *Retama sphaerocarpa* in Mediterranean grasslands. López-Pintor et al. (2006) found no difference in soil P content and pH with distance from the shrub crown. Belsky et al. (1989) found no differences in soil pH with distance from tree trunks, but a higher soil P content immediately next to the tree trunk; nevertheless, soil P content declined sharply within the canopy area (Belsky et al., 1989). Overall the results of our study were in agreement with these findings as soil P content and pH were similar between locations.

Grasses growing beneath the canopy of *P. caldenia* tended to show higher TGL than those beneath the canopy of *L. divaricata*. However, significant differences were only found in late spring 2011 for *N. clarazii*, and in late spring 2012 for both grass species (Fig. 2). This was coincident with lower soil temperatures in spring beneath the canopy of *P. caldenia* (Table 1). These results are in agreement with findings of Buschiazzo et al. (2004). These authors showed that while soil temperatures were ~35 °C beneath the canopy of *P. caldenia* during summer in the Northern Caldenal, they could reach ~65 °C in open areas. Differences in soil temperatures between locations for *P. caldenia*, but not for *L. divaricata*, may probably be attributed to differences in canopy architecture. Differences in plant architecture might account for differences in the amount of solar radiation reaching the ground, and hence, for differences in soil temperature. *Prosopis caldenia* exhibits a hemispherical canopy inclined towards the cardinal point from which the highest amount of solar radiation is received during this species growth cycle (i.e., from the south during spring and summer). However, there seems to be no specific pattern in the canopy architecture of *L. divaricata*, which shows an inverted cone shape (Cano, 1988; Kröpfl et al., 2012).

Differences in soil temperatures should be expected to turn into differences in soil water content as a result of influencing the evapotranspiration rates (Smith et al., 1994). Accordingly, soil water content has been found to be higher beneath the canopy of woody species than in open areas in the Caldenal (Llorens & Frank, 1999). However, in the present study, soil water content did not differ between the study locations (Tables 1 and 2). The only exceptions were the lower temperatures recorded beneath the canopy of *P. caldenia* in spring. This may be explained by a higher water demand from grasses due to their increased growth rate during the flowering period (Langer, 1972). This may have overridden any increase in soil water content accounted for by the shade provided by the woody species canopy. Our results are in partial agreement with those of Belsky et al. (1993). These authors, in a similar study in the African savannas, found that soil water content was higher beneath the canopy of trees than in open areas due to the lower temperatures and reduced evapotranspiration rates at the beginning of the grass growth cycle. However, with the progress of the growing season, grasses grew faster beneath the canopy of trees than in open areas, extracting increasingly greater amounts of soil water and, thereby, equalling soil water content between locations by the end of the grass growth cycle.

The lack of differences in soil water content between locations (in spite of differences in soil temperatures) can also be explained by the counterbalancing effect of the interception of precipitation by the shrub canopies during small rainfall events. Accordingly, Kröpfl et al. (2002) reported that *L. divaricata* often significantly reduced soil water availability beneath its canopy. Belsky et al. (1989) showed that the proportion of precipitation intercepted by the canopy of trees was related to the magnitude of the rainfall event, ranging from 100 to 0% for rainfall events from 2 to 20 mm, respectively.

Another possible explanation for the higher TGL of grass species beneath the canopy of *P. caldenia* and not of that of *L. divaricata* may be related to the differences found in soil N and OM content. Although not statistically significant, both soil parameters tended to be higher beneath the canopy of *P. caldenia* than that of *L. divaricata* (Table 3). This can be attributed to woody species differences in morphology and leaf habit. As discussed by Whitford et al. (1996), differences in canopy architecture (i.e., hemispherical *vs.* conical) result in differences in wind turbulence and, hence, in fine particulate and litter accumulation. These authors found that the accumulation and retention of litter was higher beneath the canopy of hemispherical than conical shrubs. Although wind turbulence and amount of litter deposition were not measured in the present study, the latter might provide an explanation for the higher N and OM content in soils beneath the hemispherical canopy of *P. caldenia* than beneath the conical canopy of *L. divaricata*. In addition, leaf habit (i.e., deciduous *vs.* evergreen species) can also affect soil N and OM content as a result of differential deposition of litter. It has been shown that leaf longevity

in deciduous trees in temperate forest range from 90 to 180 days, while leaf longevity of evergreens in temperate forests are considerably longer, often more than 500 days (Kikuzawa, 1995). The longer leaf life span on evergreen species plays an important role as a nutrient conservation mechanism, in contrast to the high resorption efficiency typical of deciduous species (Aerts, 1996). It is not yet known, however, the extent of differences in the recycling of nutrients between deciduous and evergreen woody species in the study ecosystem.

Even though incident solar radiation was not assessed in the present study, its effect on grass growth parameters cannot be overlooked. It has been demonstrated that a decrease in light intensity causes an increase in leaf length and a decrease in leaf dry weight (Langer, 1972). Data of specific leaf area (i.e., the ratio of leaf area to dry mass) should be the subject of future research to assess the extent to which grass TGL could be used as a predictor of grass productivity in the study ecosystem.

The other growth parameter evaluated in the present study (NGL) varied across time within a year and between years, but it was not affected either by woody species or by location for both grass species (Fig. 3). Overall, grass tillers hold a relatively constant number of green leaves during their growth cycle (Davies, 1977); nevertheless, NGL during the reproductive phase tended to be higher than that in the vegetative phase as a result of internode elongation. In addition, the NGL can be modified by water and nutrient availability (Longnecker & Robson, 1994). According to this, differences in NGL across time within a year and between years might be the outcome of differences in soil water content and the onset of flowering, as it was explained for TGL. On the other hand, the lack of differences in the NGL between locations can be partially attributed to their similar water content. Likewise, the differences in N and OM content between locations might have not been sufficient to trigger differences in the NGL between the study grass species.

The results of the present study are in agreement with the stress-gradient hypothesis. According to it, facilitative mechanisms would prevail over competitive ones in a semi-arid ecosystem like the Caldenal. This is because the stress imposed by the abiotic environment does not reach a threshold over which facilitation ceases. Our results contribute to the understanding of the interaction between woody and grass species. This is an essential preliminary step towards the design of woody species management strategies aimed to improve grassland productivity in semi-arid rangelands of central Argentina.

ACKNOWLEDGEMENTS

REFERENCES

Aerts, R. (1996). Nutrient Resorption from Senescing Leaves of Perennials: Are there General Patterns? *Journal of Ecology* 84: 597-608.

Belsky, A.J., R.G. Amundson, J.M. Duxbury, S.J. Riha, A.R. Ali & S.M. Mwonga (1989). The effects of trees on their physical, chemical and biological environments in a semi-arid savannah in Kenya. *Journal of Applied Ecology* 26: 1005-1024.

Belsky, A.J., S.M. Mwonga, R.G. Amundson, J.M. Duxbury & A.R. Ali (1993). Comparative effects of isolated trees on their under-canopy environments in high- and low-rainfall savannas. *Journal of Applied Ecology* 30: 143-155.

Bertness, M.D. & R.M. Callaway (1994). Positive interactions in communities. *Trends in Ecology and Evolution* 9: 191-193.

Bontti, E.E., R.M. Bóo, L.I Lindström & O.R. Elía (1999). Botanical composition of cattle and vizcacha diets in central Argentina. *Journal of Range Management* 52: 370-377.

Bóo, R.M. & D.V. Peláez (1991). Ordenamiento y clasificación de la vegetación en un área del sur del Distrito del Caldén. *Boletín de la Sociedad Argentina de Botánica* 27: 135-141.

Bóo, R.M., L.I. Lindström, O.R. Elía & M.D. Mayor (1993). Botanical composition and seasonal trends of cattle diets in central Argentina. *Journal of Range Management* 46: 479-482.

Bray, R.H. & L.T. Kurtz (1945). Determination of total, organic and available forms of phosphorous in soil. *Soil Science* 59: 39-45.

Bremner, J.M. & C.S. Mulvaney (1982). Nitrogen total. In: Page, A.L., Miller, R.H. and R.D. Keeney (Eds.). Methods of Soil Analysis. Part 2: Chemical and microbiological properties, pp. 595-624. American Society of Agronomy, Madison, USA.

Buschiazzo, D.E., H.D. Estelrich, S.B. Aimar, E. Viglizzo & F.J. Babinec (2004). Soil texture and tree coverage influence on organic matter. *Rangeland Ecology and Management* 57: 511-516.

Cabrera, A.L. (1976). Regiones fitogeográficas Argentinas In: E.F. Ferreira Sobral (Ed.), Enciclopedia Argentina de Agricultura y Jardinería, pp. 1-85. ACME, Buenos Aires, Argentina. 1408 p.

Callaway, R.M. & L.R. Walker (1997). Competition and Facilitation: A Synthetic Approach to Interactions in Plant Communities. *Ecology* 78: 1958-1965.

Cano, E. (1988). Pastizales naturales de La Pampa. Tomo I: Descripción de las especies más importantes (Convenio AACREA – Gobierno. de La Pampa y Buenos Aires).

Choler, P., R. Michalet & R.M. Callaway (2001). Facilitation and competition on gradients in alpine plant communities. *Ecology* 82: 3295–3308.

Davies, A. (1977). Structure of the grass swards. In: Proceedings of the International meeting on animal production from temperate grassland. pp. 36-44. Dublin, Ireland.

Distel, R.A. & R.M. Bóo (1996). Vegetation states and transitions in temperate semiarid rangelands of Argentina. In: West, N. (Ed.), Rangelands in a Sustainable Biosphere, pp. 117-118. Society for Range Management, Denver, USA.

Distel, R.A. & D.V. Peláez (1985). Fenología de algunas especies del Distrito del Caldén (*Prosopis caldenia* Burk.). *Instituto Nacional de Tecnología Agropecuaria IDIA* Sept-Dec.: 35-40.

Instituto Nacional de Tecnología Agropecuaria. (1980). Inventario Integrado de los Recursos Naturales de la Provincia de La Pampa. INTA, Buenos Aires, Argentina.

Kikuzawa, K. (1995). Leaf phenology as an optimal strategy for carbon gain in plants. *Canadian Journal of Botany* 73: 158-163.

Kröpfl A.I., G.A. Cecchi, N.M. Villasuso & R.A. Distel (2002). The influence of *Larrea divaricata* on soil moisture and on water status and growth of *Stipa tenuis* in southern Argentina. *Journal of Arid Environments* 52: 29-35.

Kröpfl, A.I., N.M. Villasuso & G. Peter (2012). Guía para el reconocimiento de especies de los pastizales del Monte Oriental de Patagonia. INTA, Bariloche, Argentina.

Langer, R.H.M. (1972). How Grasses Grow. Edward Arnold, London, UK.

Llorens, E. & E.O. Frank (1999). Aspectos ecológicos del estrato herbáceo del Caldenal y estrategias para su manejo. INTA, Anguil, Argentina.

Longnecker, N. & A. Robson (1994). Leaf Emergence of Spring Wheat Receiving Varying Nitrogen Supply at Different Stages of Development. *Annals of Botany* 74: 1-7.

López-Pintor, A., A. Gómez Sal & J.M. Rey Benayas (2006). Shrubs as a source of spatial heterogeneity - the case of *Retama sphaerocarpa* in Mediterranean pastures of central Spain. *Acta Oecologica* 29: 247–255.

Ludwig, F., H. De Kroon, F. Berendse & H.H.T. Prins (2004). The influence of savanna trees on nutrient, water and light availability and the understorey vegetation. *Plant Ecology* 170: 93-105.

Matthews, E. (1983). Global vegetation and land use: new high-resolution data bases for climate studies. *Journal of Climate and Applied Meteorology* 22: 474-487.

McMurtrie, R. & L. Wolf (1983). A model of competition between trees and grasses for radiation, water and nutrients. *Annals of Botany* 52: 449-458.

McNaughton, S.J. (1991). Dryland herbaceous perennials In: Mooney, H.A., Winner, W.E. & Pell, E.J. (Eds.), Response of Plants to multiple Stresses, pp. 307-328. Academic Press, New York, USA.

Pisani, J.M., R.A. Distel & E.E. Bontti (2000). Diet selection by goats on a semiarid shrubland in central Argentina. *Ecología Austral* 10: 103–108.

Saint Pierre, C. & C.A. Busso (2006). Capacidad competitiva y tolerancia a la defoliación en *Stipa clarazii*, *Stipa tenuis* y *Stipa ambigua*. *Phyton, International Journal of Experimental Botany* 75: 21-30.

Sala, O.E. (1988). The effect of herbivory on vegetation structure In: M.J.A. Werger, P.J.M. van der Aart, H.J. During and J.T.A Verhoeven (Eds.). Plant form and vegetation structure, pp. 317-330. Academic Publishing, The Hague, The Netherlans.

Sánchez, J.P. & M.A. Lazzari (1999). Impact of fire on soil nitrogen forms in Central Semiarid Argentina. *Arid Soil Research and Rehabilitation* 13: 81–90.

SAS Institute (2007). JMP User Guide, Release 7. SAS Institute: Cary, NC.

Scholes, R.J. & S.R. Archer (1997). Tree-grass interaction in savannas. *Annual Review of Ecology and Systematics* 28: 517-544.

Servicio Meteorológico Nacional (2013). Servicios climáticos: clima en Argentina. Available at: www.smn.gov.ar/serviciosclimaticos/?mod=elclima&id=72.

Smith, E.A., W.L. Crosson & B.D. Tanner (1992). Estimation of surface heat and moisture fluxes over a prairie grassland. Part 1: *In situ* energy budget measurements incorporating a cooled mirror dew point hygrometer. *Journal of Geophysical Research* 97: 557–582.

Snedecor, G.W. & W.G. Cochran (1980). Statistical Methods (7th edn.). Iowa State University Press: Ames, IA.

Walker, B.H. & I. Noy-Meir (1982). Aspects of the stability and resilience of savanna ecosystems In: B.J. Huntley and B.H. Walker (Eds.), Ecology of tropical savannas, pp. 556-590. Springer-Verlag, New York, USA.

Walkley, A. & I. Black (1934). An examination of the Degtjareff method and a proposed modification of the chromic matter and a proposed modification of the chromic acid titration method. *Soil Science* 34: 29-38.

Walter, H. (1971). Ecology of Tropical and Subtropical Vegetation. Oliver and Boyd, Edinburgh, UK.

Weltzen, J.F & M.B. Coughenour (1990). Savanna tree influence on understory vegetation and soil nutrients in northwestern Kenya. *Journal of Vegetation Science* 1: 325-334.

Werner, P.A. (1990). Ecological determinants of savannas: Abiotic and biotic. *Journal of Biogeography* 17: 401-402.

Whitford, W.G., E. Martinez-Meza & A.G. de Soyza (1996). Morphological variation in creosotebush *Larrea tridentata* affects ecosystem properties. In: J.R. Barrow, E.D. McArthur, R.E. Sosebee and R.J. Tausch (Eds.). Proceedings: Shrubland Ecosystem Dynamics in a Changing Environment. pp. 195-198. Ogden, USA.