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Effect of post-fire defoliation on growth of two native grasses in the Caldenal, Argentina

Efecto de la defoliación post-quema sobre el crecimiento de dos gramíneas nativas en el Caldenal, Argentina

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Abstract. Plant growth in semiarid rangelands may be affected by time grazing is excluded during the post-fire regeneration period. The objective of this field work was to study the effect of post-fire defoliation at different phenological stages [vegetative (early-season defoliation) and internode elongation (late-season defoliation)] on growth of *Piptochaetium napostaense* and *Poa ligularis*, two very important perennial native grasses in the temperate semi-arid region of central Argentina (Caldenal). In general, the post-fire defoliation treatments did not affect the number of green leaves on tillers of *P. napostaense*. Early-season post-fire defoliation generally reduced the number of green leaves on tillers of *P. ligularis* in comparison to those in control plants. Late-season defoliation, however, usually increased the number of green leaves on tillers of *P. ligularis*. Nevertheless, very few significant ($p<0.05$) differences were detected within either one or the other phenological stage. Height and total green length (leaves + stem + sheaths) of tillers on plants of *P. napostaense* and *P. ligularis* exposed to defoliation were lower ($p<0.05$) or similar ($p>0.05$) than values on non-defoliated plants, respectively. Immediately after early- and late-season defoliation treatments, relative growth rates for tiller height and total green length were reduced ($p<0.05$) on plants of both species with respect to control plants. Our results suggest that a one-year-period without severe defoliations after fire would be at least necessary for not risking the persistence of these perennial grasses in the Caldenal community.

Key words: *Piptochaetium napostaense*, *Poa ligularis,* Caldenal, grass growth, post-fire resting.

Resumen. El crecimiento en los pastizales naturales semiáridos puede ser afectado por la longitud de tiempo que el pastoreo es excluido durante el período de regeneración post-fuego. El objetivo de este trabajo a campo fue estudiar el efecto de la defoliación post-fuego en diferentes estados fenológicos: vegetativo (defoliación temprana) y elongación de entrenudos (defoliación tardía) sobre el crecimiento de *Piptochaetium napostaense* y *Poa ligularis*, dos gramíneas nativas perennes muy importantes en la región semiárida templada central de Argentina (Caldenal). En general, los tratamientos de defoliación post-quema no afectaron el número de hojas verdes en las macollas de *P. napostaense*. La defoliación temprana después del tratamiento de fuego generalmente redujo el número de hojas verdes en las macollas de *P. ligularis* con respecto a las plantas control. Contrariamente, la defoliación tardía usualmente incrementó el número de hojas verdes en las macollas de *P. ligularis*. Sin embargo, en ambos casos, muy pocas de las diferencias detectadas fueron significativas ($p<0,05$). La altura y la longitud verde total (láminas + tallo + vainas) de las macollas de las plantas de *P. napostaense* y *P. ligularis* expuestas a defoliación fueron menores ($p<0,05$) o similares ($p>0,05$) a aquellas de las plantas no defoliadas. Inmediatamente después de los tratamientos de defoliación temprana y tardía, las tasas de crecimiento relativas de la altura y la longitud verde total de las macollas de las plantas de ambas especies fueron reducidas ($p<0,05$) con respecto a las plantas control. Nuestros resultados sugieren que un período prolongado sin defoliaciones severas después del fuego (al menos un año) sería necesario a fin de no arriesgar la persistencia de estas gramíneas perennes en la comunidad del Caldenal.

Palabras clave: *Piptochaetium napostaense*, *Poa ligularis*, Caldenal, crecimiento de gramíneas, descanso post-fuego.

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INTRODUCTION

A high capacity for new tiller formation and high growth rates of these tillers after foliage removal contribute to determine a rapid photosynthetic canopy re-establishment, and allow perennial grasses to tolerate defoliation and maintain their status in the community (Becker et al., 1997). Removal of biomass and photosynthetic tissue by either grazing or fire may reduce perennial grass growth (Bullock, 1998; Peláez et al., 2003). Moreover, a combination of burning and immediate grazing thereafter may be even more damaging (Jirik & Bunting, 1994). Number and size of leaves, and tiller height are growth components that may contribute to re-establishment of a photosynthetic surface area. If post-fire defoliation has a negative effect on one or more of these growth components, rapid re-establishment of a green canopy might be limited. Therefore, length of the resting period after fire might affect perennial grass growth.

Piptochaetium napostaense (Speg.) Hack. and *Poa ligularis* Ness. are two cool-season perennial native grasses that are important forage resources in the temperate semi-arid region of central Argentina (known as the Caldenal: Cabrera, 1976). According to Bóo et al. (1997), a combination of repeated, moderately-severe controlled fires followed by proper livestock grazing might be a key factor for increasing the desirable grass production. During late summer or early fall, some ranchers conduct controlled burns to reduce shrub cover and improve forage production. However, allowing livestock to graze burnt forage 6 months (or less) after fire might be detrimental for rangeland grass persistence. Although some studies have investigated the effects of controlled fires (Peláez et al., 2003) and defoliation (Becker et al., 1997) on growth of perennial, forage native grasses in the southern Caldenal, information is lacking on the effects of post-fire defoliation on growth of *P. napostaense* and *P. ligularis*. This information is important to develop guidelines for a better grazing management of these species after fire which will contribute to maintain their vigor, production and persistence in the community. The objective of this field work was to study the effect of post-fire defoliation at different phenological stages [vegetative (early-season defoliation) and internode elongation (late-season defoliation)] on growth of *P. napostaense* and *P. ligularis*.

MATERIALS AND METHODS

Study Site. The study was carried out at a representative site in the southern Caldenal. It is located in the southeastern corner of La Pampa province in central Argentina (38°45´S, 63°45´W), and includes an area of 20 ha which has been closed to grazing since 1982, and had not been burnt during the last 15 years. Vegetation, climate and soil of this semiarid region have been described elsewhere (INTA et al., 1980). There is an abundant grass layer dominated by *P. ligularis*, *P. napostaense*, *Nassella clarazii* (ex *Stipa clarazii* Phil.), and *Nassella tenuis* (ex *Stipa tenuis* Phil.). Other common grasses at the study site include *Stipa ichu* (ex *S. gynerioides* Phil.) and *Stipa speciosa* Trin. et. Rupr. The dominant woody species are *Prosopis caldenia* Burk., *Prosopis flexuosa* DC., *Condalia microphylla* Cav. and *Larrea divaricata* Cav.

The soil at the site is a Calciustoll, well drained with a medium to heavy texture. A petrocalcic horizon is found at an average depth of 40-60 cm. Annual mean temperature is 15.3°C. Average annual precipitation is 400 mm, concentrated during fall and spring. Climatic data are from Río Colorado, province of Río Negro, 20 Km SW from the study site.

Fire treatment. Thirty plants of each *P. napostaense* and *P. ligularis* were selected at random within the study site and exposed to fire at the end of their growing season (28 and 30 December 2004). Fire was applied to individual plants with a portable propane burner similar to the one described by Britton & Wright (1979). Plant burners have been used successfully in several plant communities to evaluate fire effects (Robberecht & Defossé, 1995; Bunting et al., 1998; Peláez et al., 2001), and have the advantage of allowing good control of time and temperature exposures on individual plants. Fire was applied until the temperature at the meristematic crown zone reached 250-320°C. The temperatures chosen were similar to those measured during a controlled burn in the same region (Bóo et al., 1996). Temperatures were measured with thermocouples (chromel-alumel) located at the soil surface, inside the meristematic crown zone (centre of the plant), without touching the soil or the plant (Peláez et al., 1997). Temperatures were recorded at 1-s time intervals by connecting the thermocouples to a Campbell 21 XL datalogger. Temperatures were recorded until they dropped below 60°C.

Defoliation treatments. During 2005, burnt plants of *P. ligularis* and *P. napostaense* were exposed to different defoliation treatments: no defoliation (control), early-season defoliation, and late-defoliation. Each defoliation treatment was applied to 10 previously burnt plants of each species, which were clipped to approximately 2 cm above ground level. Defoliation treatments were carried out at two different phenological stages; either at the vegetative (early-season defoliation: 1 August 2005, 19 May 2006) or internode elongation (late-season defoliation: 11 October 2005; 5 October 2006) developmental stages. The same defoliation treatments were applied to the same plants in 2006.

Growth measurements. After the fire treatment in 2005, three plants of each species per post-fire defoliation treatment were selected at random; the remaining burnt plants were reserved for a bud viability study. Six tillers (three from the centre and the other three from the periphery) were selected at random from each plant and identified by placing wire loops at their bases. The number of green leaves, height and total green tiller length (i.e. length of all green lamina plus all green light-exposed sheaths plus all green stem segments per tiller) were measured on these tillers. These measurements were recorded every 15-30 days during the 2005 and 2006 growing seasons. Relative growth rates (RGR) were calculated following Hilbert et al. (1981) as RGR = $(\ln X_2 - \ln X_1) / (t_2 - t_1)$, where X was either tiller height or total green tiller length over a time interval t_1 to t_2.

Statistical analysis. All data were transformed to log (X+1) prior to statistical analysis to follow ANOVA assumptions, except tiller height data which were square-root (X+1) transformed. Comparison among defoliation treatments was analyzed separately for each species and year within each sampling date using a nested ANOVA (main factor: treatments; nested factor: plants) following a completely randomized design. The Duncan test was used to separate means when statistical differences were found (Snedecor & Cochran, 1980). Data from tillers at the centre and at the periphery were grouped for analysis since there were not statistical differences (p>0.05) among them for any study variable.

RESULTS

Number of green leaves. Tillers of defoliated *P. napostaense* plants had a similar (p>0.05) number of green leaves than those on the control plants (Fig. 1A) after both post-fire defoliation treatments during the first study year (2005). Immediately after early-season defoliation (July 7) in 2006, the number of green leaves per tiller on *P. napostaense* was lower (p<0.05) than that on control plants (Fig. 1B). Tillers of plants defoliated late in the season had a similar (p>0.05) number of green leaves as non-defoliated plants immediately after the defoliation treatment (October 27) (Fig.1B). At the end of each growth cycle, control plants and plants defoliated either early or late in the season had a similar (p>0.05) number of green leaves (Fig. 1A and 1B).

After early-season defoliation in 2005, tillers of defoliated plants of *P. ligularis* appeared to have a lower number of green leaves than those on control plants; however, no statistical differences (p>0.05) were detected (Fig. 1C). Although tillers of plants defoliated late in the season appeared to have a greater number of green leaves than controls at the end of this growth cycle (2005), no statistical differences (p>0.05) were found (Fig. 1C). During the second study period, defoliated plants had a lower (p<0.05) number of green leaves than controls (Fig. 1D) only at the first sampling date after both the early- (July 7) and late-season (October 27) defoliations. Towards the end of this study period, green leaves were only observed on tillers of plants defoliated late in the season (Fig. 1D).

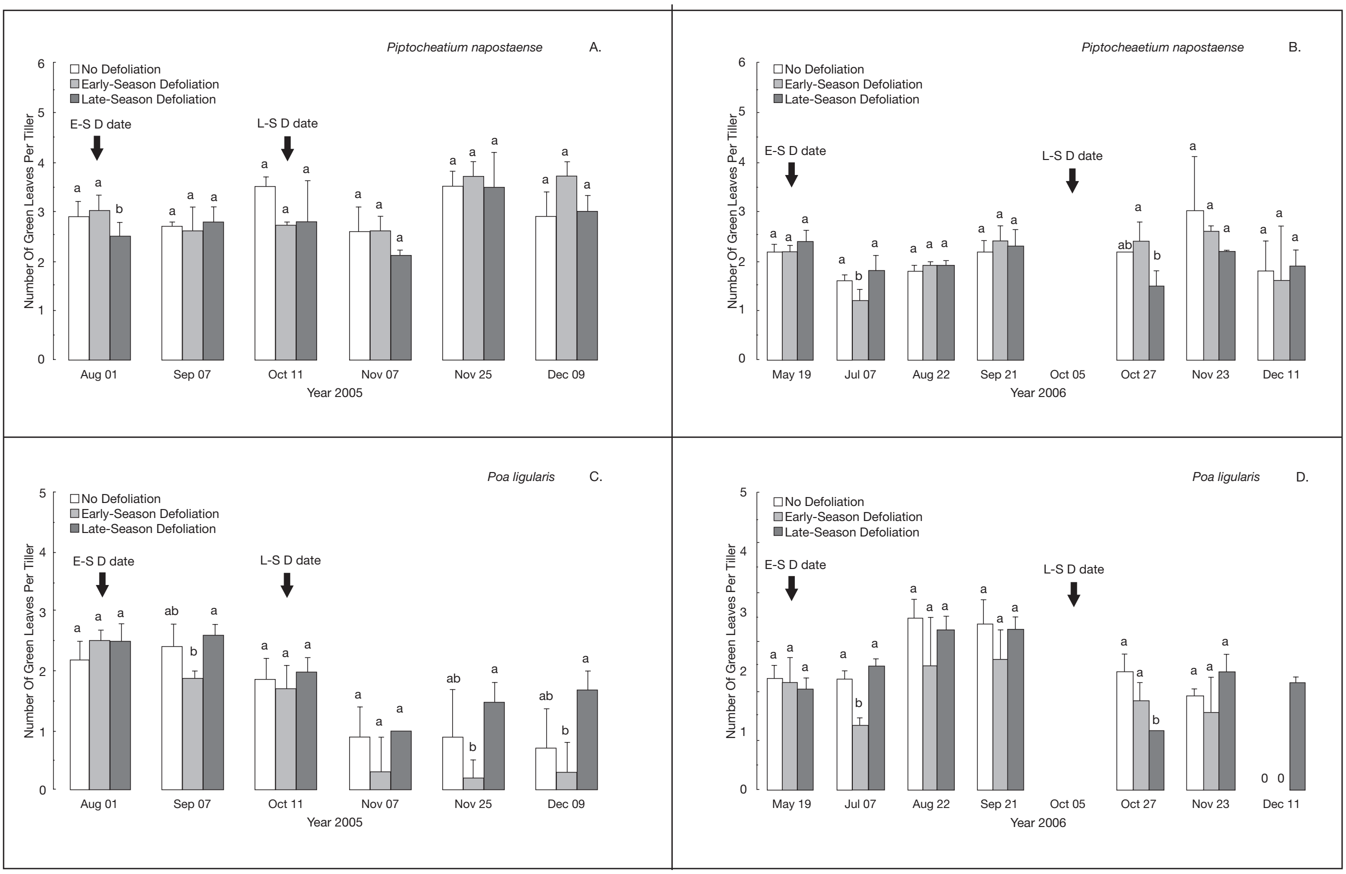
Height. In 2005, tillers on control plants of *P. napostaense* were taller (p<0.05) than those on defoliated plants after both study defoliation treatments (Fig. 2A). In 2006, this only occurred immediately after the early- (July 7) and late-season (October 27) defoliations (Fig. 2B). Thereafter, tiller height of control plants was similar (p>0.05) to that on tillers of defoliated plants (Fig. 2B). Between 7 September and 11 October 2005, relative growth rates appeared to be greater on plants defoliated early in the season than on control plants, but differences were not significant (p>0.05). A similar response was observed between 7 and 25 November for late-season defoliated plants (Fig. 3A). Similar responses were shown for early-season defoliated plants between July 7 and August 22, and for late-season defoliated plants between October 27 and November 23 in 2006 (Fig. 3A).

Tillers on plants of *P. ligularis* defoliated early in 2005 had similar (p>0.05) heights as controls; the exception was at the first sampling date after defoliation (September 7), when tillers were tallest (p<0.05) on control plants (Fig. 2C). After the late-season defoliation, tillers were shorter (p<0.05) on defoliated than on control plants (Fig. 2C). Tillers of plants defoliated early and late in the 2006 growing season were shorter (p<0.05) than those on control plants; the only exception was at the last sampling date (23 November), when they were similar (p>0.05) (Fig. 2D). Relative growth rates showed similar responses during 2005 and 2006. Tillers of defoliated plants had lower (p<0.05) relative growth rates than those on controls during the defoliation period, regardless of the defoliation treatment. However, relative growth rates were greater (p<0.05) on tillers of defoliated than on those of non-defoliated plants after the defoliation event (Fig. 3B).

Total green length. Total green length of tillers on defoliated plants of *P. napostaense* was lower (p<0.05) than that on control plants after the early-season defoliation in 2005 (Fig. 4A). A similar response was found after the late-season defoliation; however, differences were only significant (p<0.05) at the first two sampling dates after defoliation (Fig. 4A). After the early- and late-season defoliations in 2006, tillers of defoliated plants had smaller total green length than values on control plants; however, differences were not significant at any sampling date (Fig. 4B). At the end of both study periods, total green length appeared greater on tillers of late- than early-defoliated plants, but significant differences were not detected (Figs. 4A and 4B). After the early- and late-season defoliations in 2005 and 2006, relative growth rates for total green length followed a similar pattern to those for height (Fig. 3C).

Total green length of tillers of *P. ligularis* showed a similar pattern to that for height after both defoliation treatments in 2005 and 2006 (Figs. 4C and 4D). Also, relative growth rates showed similar patterns for both total green length and height (Fig. 3D).

Fig. 1. Number of green leaves per tiller of *P. napostaense* and *P. ligularis* either defoliated or not at different phenological stages (E-S D: early-season defoliation/vegetative; L-S D: late-season defoliation/internode elongation) during 2005 and 2006. In each sampling date, columns with the same letter are not significantly different (p>0.05). Each column is the mean of n=3 and vertical bars represent one S.D.
Fig. 1. Número de hojas verdes por macolla en plantas de *P. napostaense* y *P. ligularis* que fueron defoliadas o no en diferentes estadios fenológicos (E-S D: defoliación temprana/vegetativo; L-S D: defoliación tardía/elongación entrenudos) durante 2005 y 2006. En cada fecha de muestreo, las columnas que tienen igual letra no son significativamente diferentes (p>0,05). Cada columna es la media de n=3 y las barras verticales representan una D.S.



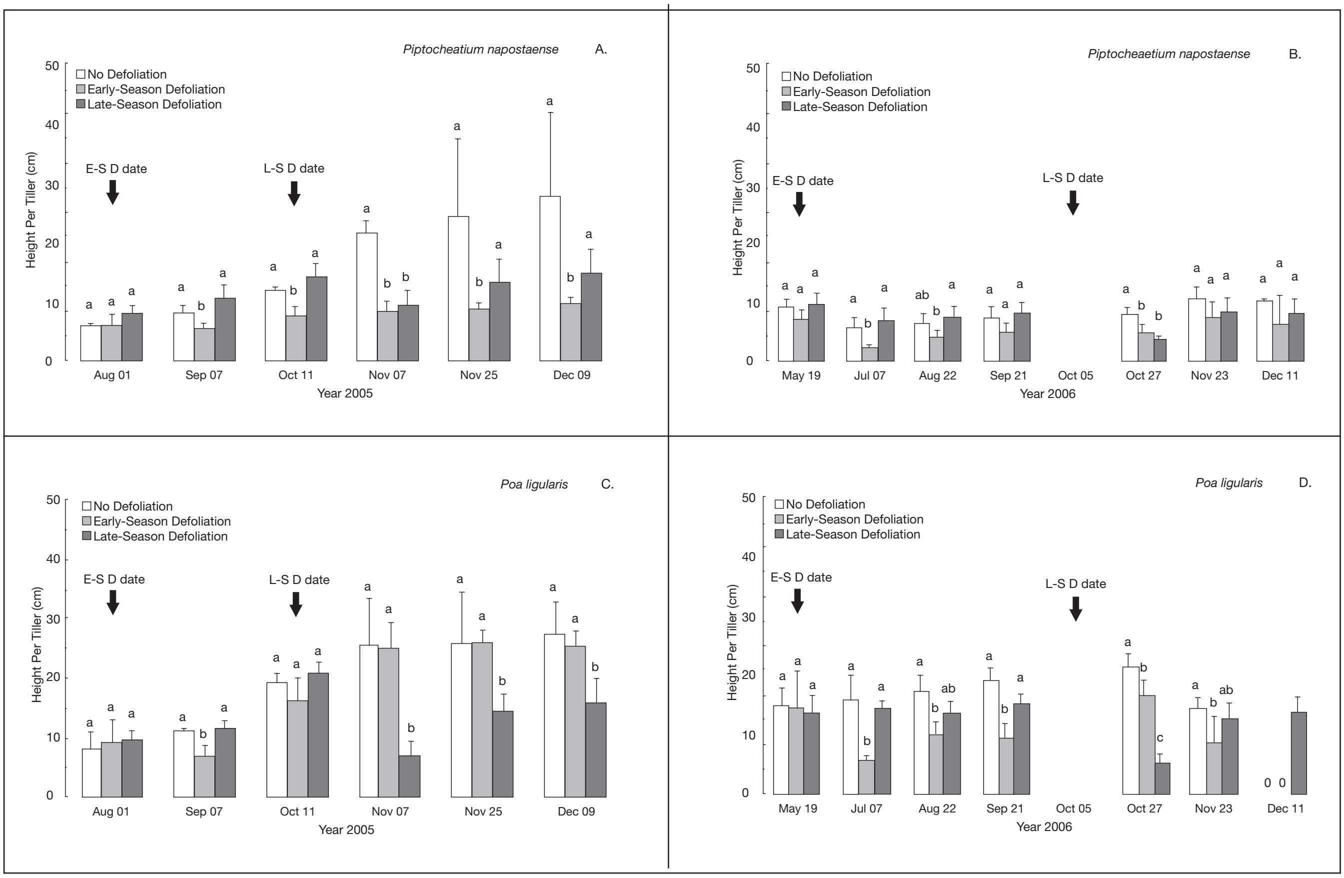
DISCUSSION

In general post-fire defoliation did not affect the number of green leaves on tillers of *P. napostaense*, except immediately after the early-season defoliation treatment effected in 2006 (Figs. 1A and 1B). Early-season defoliation after fire treatment generally reduced the number of green leaves on tillers of *P. ligularis* in comparison to control plants (Figs. 1C and 1D). On the contrary, the late-season defoliation usually increased the number of green leaves on tillers of *P. ligularis* (Figs. 1C and 1D). However, in both cases, very few of the observed differences were significant ($p<0.05$). Several studies have reported a diversity of responses in leaf appearance rates after severe defoliation in perennial grasses. Davies (1974) and Chapman et al. (1983) reported reductions of leaf number after severe defoliations in *Lolium perenne* and *Agrostis* spp. These responses were associated with defoliation at late phenological stages and with high temperatures and low soil moisture contents which occurred at that time. Other authors have reported that tillers of plants of *P. napostaense* defoliated either at different phenological stages (Becker et al., 1997) or exposed to different fire temperature regimes (Peláez et al., 2003) had similar or greater green leaf numbers than control plants. Briske & Richards (1994) suggested that increases in leaf area after severe defoliations might be associated with partitioning a greater proportion of photoassimilates to new leaf production rather than to support structures.

Peláez et al. (2003) reported that relative growth rates for height and total green length were greater on tillers of burned plants of *P. napostaense* than on those of unburned plants. Increases of growth rates on plant regrowth after burning could be caused by a (1) temporary increase of the diurnal air temperature, (2) sudden increase in nutrient availability in ashes, (3) temporary removal of competition from undesirable vegetation, (4) production of a dense crown with leaves of high photosynthetic capacity and/or (5) reduction in seed production (Whelan, 1995). Tillers of *P. napostaense* have shown greater relative growth rates for

Fig. 2. Tiller height of *P. napostaense* and *P. ligularis* plants that were defoliated or not at different phenological stages (E-S D: early-season defoliation/vegetative; L-S D: late-season defoliation/internode elongation) during 2005 and 2006. In each sampling date, columns with the same letter are not significantly different (p>0.05). Each column is the mean of n=3 and vertical bars represent one S.D.

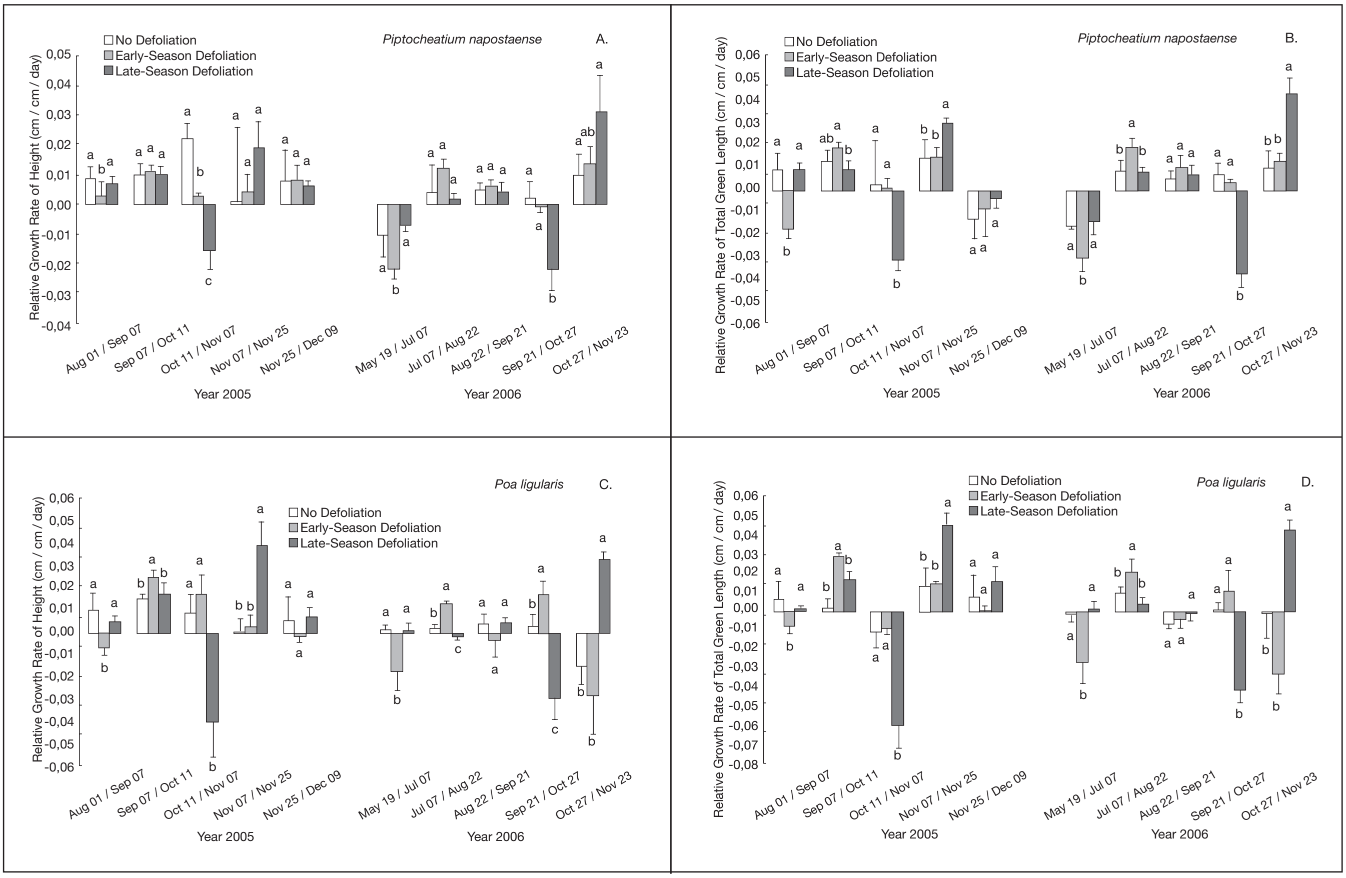
Fig. 2. Altura de las macollas en plantas de *P. napostaense* y *P. ligularis* que fueron defoliadas o no en diferentes estadios fenológicos (E-S D: defoliación temprana/vegetativo; L-S D: defoliación tardía/elongación entrenudos) durante 2005 y 2006. En cada fecha de muestreo, las columnas que tienen igual letra no son significativamente diferentes (p>0,05). Cada columna es la media de n=3 y las barras verticales representan una D.S.



height and total leaf green length after they had been defoliated at the vegetative and/or early internode elongation stages than when they were not defoliated or defoliation occurred late in the growing season (Becker et al., 1997). Several studies on perennial grasses have reported increases in relative growth rates after defoliation; this response has been attributed to (1) the development of compensatory leaf photosynthesis, (2) increases in tissue longevity or (3) enhancement of water status in the defoliated plants (Lemaire & Chapman, 1998). Enhanced leaf and tiller growth rates usually persist for only a few weeks after defoliation, and are not consistently expressed under all environmental conditions or growth periods (Richards, 1993). We found that relative growth rates for both tiller height and total green length were reduced ($p<0.05$) on burned plants of *P. napostaense* (Figs. 3A and 3C) and *P. ligularis* (Figs. 3B and 3D) with respect to controls immediately after early- and late-season defoliation treatments. This contributes to explain, at least in part, the height and total green length responses observed on tillers of both grass species. In general, tiller height and total green length on burned plants of *P. napostaense* (Figs. 2A, 2B, 4A and 4B) and *P. ligularis* (Figs. 2C, 2D, 4C and 4D) exposed to defoliation were lower ($p<0.05$) or similar ($p>0.05$) than those on non-defoliated plants. Moreover, drought conditions in the region during the study period may have intensified the effects of post-fire defoliation on plants of both perennial grasses. Regional average annual rainfall is 400mm. However, annual rainfall in the study region during 2005 and 2006 was 332 mm and 292 mm, respectively. Abiotic conditions that limit resource (water, light, nutrients) availability either before or after defoliation can have a decisive effect on the plant's ability to recover from defoliation (Richards, 1993). Jirik & Bunting (1994) mentioned that perennial grass response to defoliation after fire would be more favorable with either average or above average rainfall.

Plants of *P. napostaense* defoliated during early developmental stages had greater forage production than

Fig. 3. Tiller relative growth rates for height and total green length (blades + stem + sheaths) on *P. napostaense* and *P. ligularis* plants that were defoliated or not at different phenological stages during 2005 and 2006. In each sampling date, columns with the same letter are not significantly different (p>0.05). Each column is the mean of n=3 and vertical bars represent one S.D.
Fig. 3. Tasa de crecimiento relativa de la altura y longitud verde total (láminas + tallo + vainas) de macollas en *P. napostaense* y *P. ligularis* que fueron defoliadas o no en diferentes estadios fenológicos durante 2005 y 2006. En cada fecha de muestreo, las columnas que tienen igual letra no son significativamente diferentes (p>0,05). Cada columna es la media de n=3 y las barras verticales representan una D.S.



either non-defoliated plants or plants defoliated later in the growing season. The observed growth stimulation after plants were defoliated at the vegetative stage helps to explain this response (see also Becker et al., 1997). The potential mechanisms that are capable of increasing plant growth following defoliation can be suppressed in direct proportion to the frequency and intensity of defoliation (Briske, 1998). In general, our results suggest that the combined effects of fire and either early- or late-season severe defoliation within the first year after fire may have a negative impact on growth components of *P. napostaense* and *P. ligularis*. Although at a different magnitude, this effect persisted in the second year after fire. Consequently, this may delay the recovery of a photosynthetic canopy in the study species, which may affect their production, survival and persistence in the rangeland community. It is certain that the decision of either to graze or not vegetation after fire may vary from one site to another depending on many variables. However, results obtained in this study indicate that an extended period (at least one year) without severe defoliations after fire would be necessary to preserve the desirable vegetation (i.e., both study grass species). This is particularly important in years with below average rainfall after fire. More detailed studies are necessary to further elucidate the effects of post-fire defoliation on growth of *P. napostaense*, *P. ligularis* and other perennial grass species to establish appropriate guidelines for managing grazing after fire in the Caldenal region.

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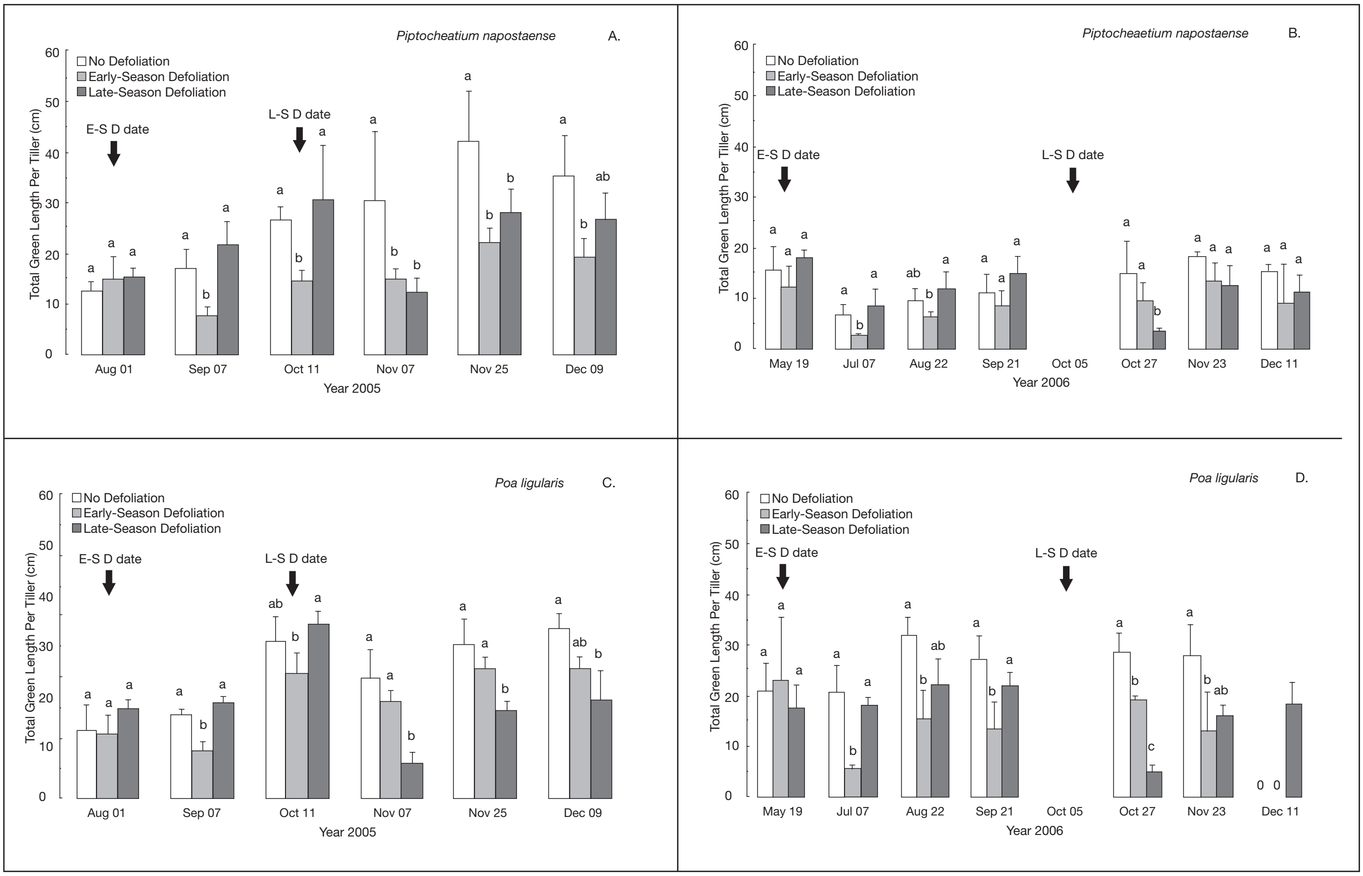
Fig. 4. Tiller total green length (blades + stem + sheaths) on *P. napostaense* and *P. ligularis* plants that were defoliated or not at different phenological stages (E-S D: early-season defoliation/vegetative; L-S D: late-season defoliation /internode elongation) during 2005 and 2006. In each sampling date, columns with the same letter are not significantly different (p>0.05). Each column is the mean of n=3 and vertical bars represent one S.D.
Fig. 4. Longitud verde total (láminas + tallo + vainas) de macollas en plantas de *P. napostaense* y *P. ligularis* que fueron defoliadas o no en diferentes estadios fenológicos (E-S D: defoliación temprana/vegetativo; L-S D: defoliación tardía/elongación entrenudos) durante 2005 y 2006. En cada fecha de muestreo, las columnas que tienen igual letra no son significativamente diferentes (p>0,05). Cada columna es la media de n=3 y las barras verticales representan una D.S.



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