

## Adequate management of post-fire defoliation would not affect the metabolic activity of axillary buds in grasses

Leticia S. Ithurrart<sup>1</sup>, Carlos A. Busso<sup>1,\*</sup>, Yanina A. Torres<sup>2</sup>, Hugo D. Giorgetti<sup>3</sup>, Gustavo D. Rodriguez<sup>3</sup> & Mariela L. Ambrosino<sup>4</sup>

<sup>1</sup> Dpto. Agronomía — CERZOS [Consejo Nacional de Investigaciones Científicas y Técnicas de la República Argentina (CONICET)], Universidad Nacional del Sur (UNS), San Andrés 800, AR-8000 Bahía Blanca, Argentina (\*corresponding author's e-mail: carlosbusso1@gmail.com)

<sup>2</sup> Dpto. Agronomía, Universidad Nacional del Sur (UNS), CIC (Comisión de Investigaciones Científicas de la Provincia de Buenos Aires), San Andrés 800, AR-8000 Bahía Blanca, Argentina

<sup>3</sup> Chacra Experimental Patagones, Ministerio de Asuntos Agrarios, Olivera 67, AR-8504 Carmen de Patagones, Argentina

<sup>4</sup> CERZOS (CONICET), Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, Ruta Nacional 35, km 334, AR-6300 Santa Rosa, Argentina

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Controlled burning is often used to improve plant structure on rangelands adapted to fire. However, possible damage resulting from post-fire grazing to reappearing desirable plant species may be a serious issue hindering usage of this method. Axillary buds are essential for the re-establishment of the photosynthetic leaf area. We studied if post-burn defoliation affects the number of axillary buds and/or their metabolic activity in *Poa ligularis*, *Nassella tenuis* (both desirable plant species) and *Amelichloa ambigua* (undesirable plant species). We found that the treatments limited neither bud production nor their metabolic activity. The greatest number of total and viable buds in the studied plant species was recorded at the vegetative stage. *Poa ligularis* had the lowest bud number per tiller but the greatest per plant. Our results thus indicate that moderate defoliation after controlled burning does not affect the survival and productivity of the desirable species.

### Introduction

Approximately 75% of the area of continental Argentina is subject to grazing by livestock (Busso & Fernández 2018). In addition to grazing, various abiotic factors (e.g., fire) are also at play, determining the current and future composition of the vegetation (Anderson 1984). Natural and artificial factors both affect the ecosystems

and hence they should be taken into account if a sustainable use of renewable natural resources is the target (Kunst 2011).

Axillary buds secure continuity of perennial grasses, being a source for tiller production (Hyder 1974). During vegetative growth, axillary buds remain either at the soil surface level or are barely buried in the soil because in grasses the nodes are at the tiller bases (Hyder 1972,

Jewiss 1972). However, when the apical meristem is transformed from vegetative to reproductive, internode lengthening raises the apex above the soil surface. This increases the possibility for such apex to be removed in a defoliation event (Briske 1991). Apex removal by e.g., grazing, activates basal axillary buds that grow and develop into tillers (Gillet 1984). If the apex is not removed, the apical dominance is maintained, and growth and development from basal, axillary buds is not stimulated (Gillet 1984). Murphy and Briske (1992) review major hypotheses proposed to explain physiological mechanisms responsible for apical dominance.

Fire and defoliation by grazing are common disturbances in arid and semiarid ecosystems worldwide (Axelrod 1985). The amount and the type (intercalary, apical, axillary meristems) of the tissue removed by fire with or without defoliation are the most important factors that determine the effects of such disturbances on plants and affect their subsequent re-establishment (Briske 1991, Richards 1993, Klimesová & Klimes 2007). Regeneration of the photosynthetic surface area is fastest from intercalary meristems, intermediate from apical meristems, and slowest from axillary buds (Briske 1991, van Loo 1992, Briske & Richards 1995, Lennartsson *et al.* 1997, Russell & Vermeire 2015). If plant intercalary and apical, active meristems are removed as a result of disturbance, regeneration of a photosynthetic canopy will depend on growth of axillary buds into tillers. However, the regrowth potential of any species might be affected if either the number or viability or both of axillary buds were reduced by those disturbances (Zammit 1988, Busso *et al.* 1989).

Individuals of several species are able to maintain bud production per tiller at a constant level regardless of previous grazing (Hendrickson & Briske 1997, N'Guessan & Hartnett 2011). However, bud production can be either reduced or dormancy increased if tillers are damaged or resources are limited during the period of maximum growth and bud formation (Vanderweide 2013). As a result, changes in tiller density and size may affect the annual bud production, and hence the tiller recruitment in the following year, which in turn affects the above-ground biomass production.

Fire removes litter and existing vegetation (Hulbert 1969) thus increasing illumination of the soil surface. As a result, the soil-surface temperature increases (Knapp *et al.* 1998), and the spectrum of light (red-to-infrared ratio) reaching the soil surface becomes altered (Willems 1983) stimulating growth and development of buds into tillers (cf. Svejcar 1990, Tomlinson & O'Connor 2004). The bud bank is replaced as a result of high plant productivity due to an increase in the rate of tillering in recently burnt areas (Benson *et al.* 2004).

Controlled burning followed by adequate grazing can increase plant production (Bóo *et al.* 1997). However, severe and frequent defoliation events can compromise perenniality through reduction of the plant photosynthetic capacity, and thus available energy for the production and development of axillary buds (Hyder 1972).

Wright and Bailey (1982) reported that during fire events in grasses, high temperatures persist for longer if the amount of dry plant material is considerable. This is because burning starts at the plant periphery, and the burning intensity is proportional to the plant basal area. This in turn can damage basal buds in plants of greater sizes. Therefore, the effects of the same level of fire disturbance on plants of different sizes (e.g., basal area, tiller number, above-ground biomass) may differ substantially.

Successful grassland management consists of planned application and manipulation of disturbances to which plant communities are adapted (Whisenant 1999). However, the extent to which such disturbances affect plant communities or individual species remains uncertain (Limb *et al.* 2011). There are several studies on the effects of fire or defoliation on perennial grass species (Busso *et al.* 1993, Benson *et al.* 2004, Dalgleish & Hartnett 2009, Russell & Vermeire 2015). However, only few (Peláez *et al.* 2009, Russell *et al.* 2013) analyzed the effects of different levels of defoliation after fire which is essential for predicting plant responses.

*Poa ligularis*, *Nassella tenuis* and *Amelichloa ambigua*, selected as our study plants, are grasses with an autumn–winter–spring developmental cycle, abundant in the temperate, semi-arid rangelands of Argentina. Through observation and measurements, we found that in our

study area *P. ligularis* had a greater basal area as compared with that of the other species.

We hypothesized that (1) defoliation would not affect the growth apex and thus would increase the number of buds per tiller in the vegetative stage; this is because the internodes are compressed keeping the apical buds close to the ground, below the height of cutting or grazing; (2) recurring defoliations after a fire event would result in a reduction in the metabolic activity of the axillary buds due to the decrease in photosynthesis of defoliated plants; and (3) applied disturbances would affect the study species in the similar way. As tillers of *P. ligularis* have a lower number of metabolically active axillary buds because plants of this species burn at higher temperatures as a result of greater size of their basal areas, we also analyzed the effects of defoliation after a controlled burning at the vegetative and/or internode-elongation stages during the second, or the first and the second post-fire years on (1) the total number of buds, and (2) the metabolic activity of buds in all the studied grass species.

## Material and methods

### Study site

The study was conducted in 2011 and 2012, within a livestock enclosure in Chacra Experimental Patagones located in the southwestern part of Buenos Aires Province (40°39'49.7'S, 62°53'6.4'W; 40 m a.s.l.), belonging to the Phytogeographical Province of the Monte (Cabrera 1976).

### Climate

The climate in the study area is temperate, semi-arid, with rainfalls occurring mainly in summer and autumn. The mean annual precipitation in 1981–2012 was 421 mm, with the minimum and maximum of 196 and 877 mm in 2009 and 1984, respectively (O. Montenegro, Chacra Experimental Patagones, Ministerio de Asuntos Agrarios de la Provincia de Bs. As., pers. comm.). During the study years, the annual precipitation was 444 and 513 mm in 2011 and

2012, respectively; and the mean annual air temperature in both years 15 °C (data from the meteorological station located at the study site). The mean monthly maximum and minimum soil temperatures (January = summer, July = winter) were 23.1 °C and 6.2 °C, respectively, in 2011; and 24.6 °C and 3.9 °C, respectively, in 2012. The mean monthly maximum relative humidity in 1981–2012 was 77.9% in July and 55.1% in December (late spring and early summer).

### Soil

The study area is predominantly flat with occasional knolls and isolated microdepressions. Fine sands carried by winds, are deposited on tosca, and loamy-sandy, weakly consolidated older materials (INTA-CIRN 1989). The soil was classified as Haplocalcid (N.M. Amiotti, Dpto. de Agronomía UNSur, pers. comm.) with mean pH of 7.

### Vegetation

The plant community in the study area includes herbaceous species of different quality for livestock production (Giorgetti *et al.* 1997). *Poa ligularis* (a highly competitive species; Distel & Bóo 1996), *Nassella tenuis* (an intermediate competitive species; Saint Pierre *et al.* 2002) and *Amelichloa ambigua* (a low competitive species; Saint Pierre *et al.* 2002) are three C<sub>3</sub> native perennial grasses in the Phytogeographical Province of the Monte, Argentina. Of the total area of this Province, approximately 554 138 ha is in Partido de Patagones (Province of Buenos Aires). Dominance of these species in the community depends, at least in part, on the grazing history and frequency and intensity of fires (Distel & Bóo 1996). In the south of this region grazing is continuous and numbers of livestock very high (Bóo & Peláez 1991). Preference of grazing animals for *A. ambigua* is low (Cano 1988) while *N. tenuis* and *P. ligularis* are highly preferred. As a result, *N. tenuis* and *P. ligularis*, more-competitive species than *A. ambigua*, are under constant grazing pressure at different phases of their developmental stages after accidental fires.

## Experimental design

We followed a randomized experimental design with balanced replicates ( $n = 6$ ). At the study site, 42 vegetation plots (1-m<sup>2</sup> each) were selected for each study species (42 × 3 species = 144 plots). Each plot containing at least six adult plants of one of the study species, constituted an experimental unit. Of the 144 plots, 126 were burned and either (1) not defoliated, or (2) defoliated in the second study year, or in the first and the second study years after controlled burning. The 18 remaining unburned plots were not defoliated.

## Treatments

We applied eight treatments. Each treatment consisted of a combination of burning, either without or with defoliation at the vegetative or internode-elongation or both developmental stages during the second, or the first and second study years. Vegetation plots which were neither burned nor defoliated were used as a control (Table 1).

## Controlled burning

Controlled burning was conducted on 23 March 2011 in an area that included 126 plots. Temperatures during burning were measured with eight type-K (chromel–alumel) thermocouples at one-second intervals. The thermocouples were

**Table 1.** Treatments applied to the plots with *P. ligularis*, *N. tenuis* and *A. ambigua* during the study years (2011 and 2012). Abbreviations: UB = unburnt, B = burnt, UD = undefoliated, DV = defoliated at the vegetative stage, DE = defoliated during internode elongation, D(V + E) = defoliated at the vegetative + internode-elongation stages.

Treatments	2011	2012
1 (control)	UB + UD	UD
2	B + UD	UD
3	B + UD	DV
4	B + UD	DE
5	B + UD	D(V + E)
6	B + DV	DV
7	B + DE	DE
8	B + D(V + E)	D(V + E)

placed at the soil-surface level but not touching the soil, in areas with high, intermediate and low fine-fuel concentrations. Temperatures were registered by a Campbell 21 XL datalogger connected to the thermocouples and buried in the soil at approx. 1-m depth. Wind speed, air temperature and relative humidity during burning were also measured at the site.

Prior to burning, we determined the amount of fine fuel (i.e., plant material, including litter, with the diameter  $\leq 3$  mm on and above the soil surface). This plant material was first collected from ten 1-m<sup>2</sup> plots, and then dried in an oven at 70 °C for 72 h. Soil moisture was determined gravimetrically in the top 10 cm of soil following Brown (1995).

The air temperature during burning (between 12:30 and 13:00 hrs) was 21.8–22.4 °C, relative air humidity 28%, and wind speed (wind direction: NW–WNW) 19.3–20 km h<sup>-1</sup>. The soil moisture content was 5%  $\pm$  1.51% (mean  $\pm$  SD,  $n = 14$ ). Fine-fuel amount was estimated to be 3.9 t dry matter per ha, and its moisture content to be 9.1%  $\pm$  4.64% (mean  $\pm$  SD,  $n = 10$ ). The maximum recorded soil surface temperature during burning was 560 °C (cf. Fig. 1).

## Defoliation

Plants were defoliated to the stubble height of 5 cm from the soil surface at the following developmental stages: (1) vegetative (15 Aug. 2011 and 6 May 2012), or (2) internode elongation (14 Oct. 2011 and 14 Sep. 2012), or (3) vegetative and internode elongation (cf. Table 1). At the end of each growing cycle (6 Jan. 2012 and 20 Dec. 2012), plants were defoliated once again to the 5-cm stubble height to obtain the total plant biomass production. After each defoliation, the plant material was oven-dried (at 70 °C for 72 h) and weighed. Neighbouring plants were also burned and/or defoliated similarly to those measured to provide a uniform competitive environment.

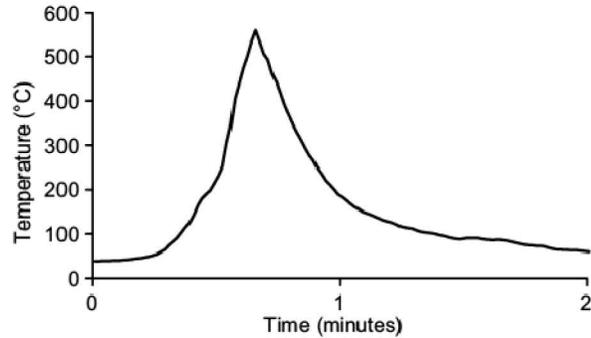
## Measurements

Sampling was done 20–30 days after each defoliation during the second growing season after the

controlled burning. On each sampling occasion, a tiller with at least one green leaf was taken from an intermediate position (between centre and periphery) on each plant. The number of total, metabolically active, dormant and/or dead buds on each tiller base was determined following Busso *et al.* (2015). A bud was considered metabolically active when the apex stained pink or red, indicating an enzymatic reduction of the tetrazolium salt (colourless) to insoluble formazan (red) (cf. Fig. 2A). Buds that remained unstained (either dormant or dead; cf. Fig. 2B) were cut into longitudinal sections and tested using Evans Blue after incubation in the TTC solution. The coloured sections were then mounted in water and examined under a microscope (Leica ICC50 with and immersion objective, 1000× magnification). Bud tissues which remained uncoloured with Evans Blue were classified as dormant (viable; Fig. 2C), while those which stained dark blue were considered dead (cf. Fig. 2D).

### Statistical analyses

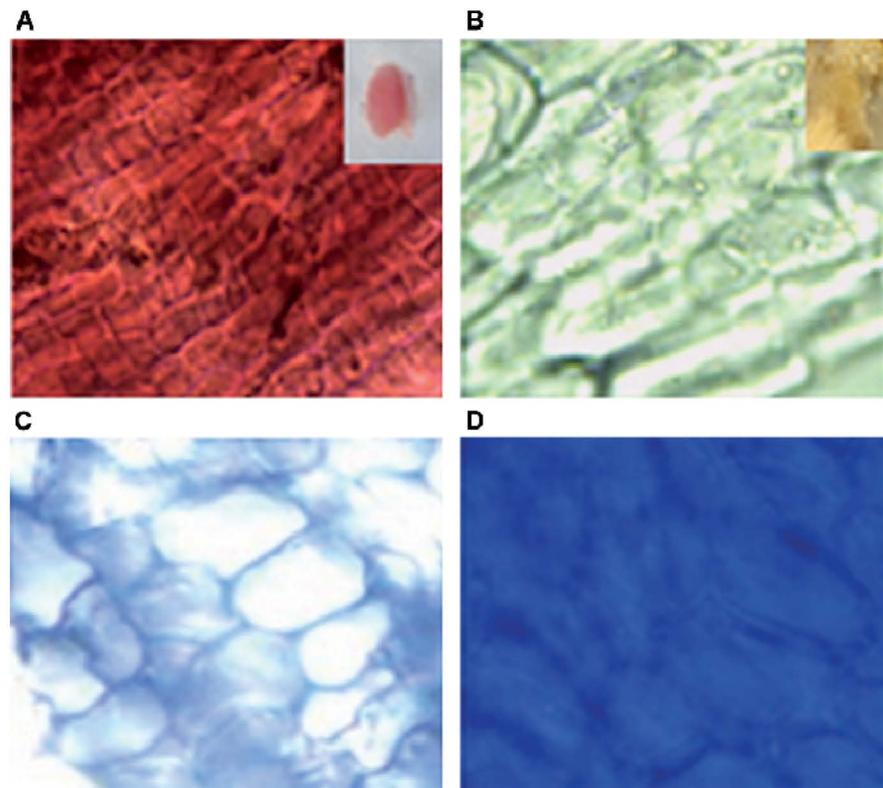
Prior to analysis, the data were  $\sqrt{(x+1)}$ -trans-



**Fig. 1.** Time–temperature curve at the soil surface during the controlled fire treatment. Temperature readings were taken once a second using eight type K thermocouples connected to a datalogger Campbell 21XL. Averages of eight measurements were used to plot the curve.

formed to meet the normality and homocedasticity assumptions. Differences in the numbers of buds per tiller were tested with split-plot ANOVA with species and treatment as major plots and sampling date as subplot.

Bud metabolic activity was also analyzed with split-plot ANOVA with species and treatment as major plots, and sampling time and bud category (i.e., metabolically active, dormant, dead) as subplots. Dormant buds were included



**Fig. 2.** Photographs of longitudinal cuts of buds of *Amelichloa ambigua* taken under a microscope (1000× magnification). (A) viable cells with high metabolic activity (stained red with TTC), (B) cells with either low or no metabolic activity (did not stain with TTC), (C) viable but dormant cells (unstained with TTC and thereafter remained uncolored with Evans Blue), and (D) dead cells (stained dark blue in Evans Blue).

in the metabolically active category because of their low number. Whenever significant differences were detected, pairwise comparisons were carried out using Tukey's test. All the analyses were performed using InfoStat (<https://www.infostat.com.ar/>).

## Results

### Number of buds per tiller

There were no significant interactions among the factors considered ( $F_{14,134} = 0.52, p = 0.9179$ ) and there was no treatment effect ( $F_{7,120} = 0.95, p = 0.4692$ ); that is, none of the combinations of controlled burning and defoliation affected the bud number per tiller. *Nassella tenuis* had 19% more tiller buds than *A. ambigua*, and *A. ambigua* had 30% more tiller buds than *P. ligularis* ( $F_{2,120} = 16.89, p < 0.0001$ ; cf. Table 2), all differences between species being significant (Tukey's test:  $p < 0.05$ ). The studied plants had 1.35 more tiller buds at the vegetative than at the internode-elongation stages ( $F_{1,134} = 12.03, p = 0.0007$ ; cf. Table 2), the differences between stages being significant (Tukey's test:  $p < 0.05$ ).

### Bud metabolic activity per tiller

All three species had at least three times more metabolically active than dead buds ( $F_{2,374} = 5.48, p = 0.0045$ ; cf. Table 3), the differences being significant (Tukey's test:  $p < 0.05$ ). At the vegetative and internode-elongation stages there were 13.6 and 1.9 times more metaboli-

cally active than dead buds, respectively ( $F_{1,374} = 54.77, p < 0.0001$ ; cf. Table 3), the differences being significant (Tukey's test:  $p < 0.05$ ). The number of metabolically active buds in *A. ambigua* and *N. tenuis* was 39.5% higher than that in *P. ligularis*, the difference being significant (Tukey's test:  $p < 0.05$ ). However, the three species did not differ significantly in the number of dead buds (cf. Table 3).

Following the developmental stage transition from vegetative to internode elongation, the number of metabolically active buds decreased by 47.8%, and simultaneously the number of dead buds increased 3.7 times (cf. Table 3), the differences between stages being significant (Tukey's test:  $p < 0.05$ ).

### Total, and metabolically active buds per plant

There was no effect of treatment on either the number of all buds or the number of metabolically active buds. *Poa ligularis* doubled the number of all buds, and had 3.5 times more metabolically active buds than the other two species ( $F_{2,285} = 2.95, p = 0.05$ ; cf. Table 4), the difference being significant (Tukey's test:  $p < 0.05$ ). Additionally, in all three species the numbers of all buds and metabolically active buds were greater by 57% and 70% at the vegetative stage than at the internode-elongation stage, respectively ( $F_{1,286} = 12.94, p = 0.0004$  and  $F_{1,286} = 18.10, p < 0.0001$ , respectively; cf. Table 4), the

**Table 3.** Numbers (mean  $\pm$  SD) of metabolically active and dead buds at the stem base of each tiller in each species and at each developmental stage.

**Table 2.** Bud numbers (mean  $\pm$  SD) at the stem base of each tiller in each species and at each developmental stage.

	Bud no. $\pm$ SD
<b>Species</b> (total $n = 96$ )	
<i>Poa ligularis</i>	0.91 $\pm$ 0.93
<i>Amelichloa ambigua</i>	1.3 $\pm$ 0.99
<i>Nassella tenuis</i>	1.6 $\pm$ 0.86
<b>Stage</b> (total $n = 144$ )	
Vegetative	1.46 $\pm$ 0.95
Internode elongation	1.08 $\pm$ 0.95

	Bud no. $\pm$ SD at the stem base of each tiller	
	metabolically active	dead
<b>Species</b> (total $n = 96$ )		
<i>Poa ligularis</i>	0.72 $\pm$ 0.89	0.19 $\pm$ 0.44
<i>Amelichloa ambigua</i>	1.14 $\pm$ 0.97	0.16 $\pm$ 0.47
<i>Nassella tenuis</i>	1.25 $\pm$ 0.85	0.35 $\pm$ 0.73
<b>Stage</b> (total $n = 144$ )		
Vegetative	1.36 $\pm$ 0.98	0.10 $\pm$ 0.32
Internode elongation	0.71 $\pm$ 0.75	0.37 $\pm$ 0.71

differences being significant (Tukey's test:  $p < 0.05$ ).

## Discussion

In agreement with the first hypothesis, tillers of the three studied species had the highest numbers of all buds and metabolically active buds in June (i.e., in the vegetative stage). The lowest numbers were recorded in October (i.e., in the reproductive stage). The opposite was true for the dead buds. Similar was found by Flemmer *et al.* (2002) in *Nassella longiglumis*, *N. tenuis* and *Jarava ichu*. They found the greatest number of buds between April and June (metabolically active buds) and in October (dead buds). Their lowest numbers were found between October and December (metabolically active buds) and between April and June (dead buds).

Apical meristems are crucial for the meristematic potential of perennial grasses because they are the source of phytomers and their axillary buds. These axillary buds may develop into adult tillers during the same growing season, thus producing successive axillary buds (Stubbenieck & Burzlaff 1970, Briske & Noy-Meyr 1997). This sustained production of new tillers with the corresponding axillary buds could explain greater numbers of buds found in June, during the tillering stage of the studied species. Floral induction, in response to photoperiod stimulus, marks the transition of the apical meristem from the vegetative to the reproductive stage (Langer 1972). The leaf and axillary bud primordia differentiate rapidly giving to the meristematic apex a double wrinkle appearance. While the spikelet primordia differentiate from the axillary buds, leaf primordia remain inhibited halting additional vegetative development. Vegetative growth can occur only from immature intercalary meristems of existing phytomers or from previously differentiated axillary buds in reproductive tillers (Briske 1991). Due to this, and because apical dominance was not eliminated during a defoliation event, a lower bud number could be expected during the reproductive developmental morphology stage.

Contrary to the second hypothesis, neither the reduction in the number of all buds

nor in their metabolic activity were recorded with an increasing number of defoliations. This would suggest that after exposure to moderate disturbance, the studied species were able to rebuild their photosynthetic surfaces. Indeed, after burning and grazing used in this study, dry matter production (mean  $\pm$  SD,  $n = 48$ ) remained similar ( $p > 0.05$ ) in all studied species (*P. ligularis*:  $19.67 \pm 15.32$  g per plant, *N. tenuis*:  $6.17 \pm 0.64$  g per plant, *A. ambigua*:  $23.36 \pm 2.25$  g per plant). This indicates that appropriate application of defoliation treatments after fire would not damage these species. Similar was reported for tillers of unburned *P. ligularis* which was exposed to different defoliation treatments (Busso *et al.* 2011), and for burned and defoliated tillers of *P. ligularis* and *Piptochaetium napostaense* during the vegetative or internode-elongation stage (Peláez *et al.* 2009). Nevertheless, Souto *et al.* (2004) reported that by the end of the growing season, tillers of unburned *P. ligularis* that had been defoliated more than three times, had a lower number of metabolically active axillary buds than tillers not subject to defoliation. They suggested that a high defoliation frequency would increase the number of dormant and/or dead buds in the stem bases of this species.

Regarding the third hypothesis, no differences were found among species after experimental treatment. This might be because the species were likely adapted to the applied disturbance levels. *Poa ligularis*, *A. ambigua* and *N. tenuis* had greater numbers of metabolically

**Table 4.** Numbers (mean  $\pm$  SD) of all buds and metabolically active buds per plant in each species and at each developmental stage.

	Bud no. $\pm$ SD per plant	
	all	metabolically active
<b>Species (total <math>n = 96</math>)</b>		
<i>Poa ligularis</i>	308.65 $\pm$ 649.92	264.08 $\pm$ 644.14
<i>Amelichloa ambigua</i>	163.23 $\pm$ 180.24	143.66 $\pm$ 174.11
<i>Nassella tenuis</i>	170.63 $\pm$ 218.81	140.71 $\pm$ 198.00
<b>Stage (total <math>n = 144</math>)</b>		
Vegetative	300.03 $\pm$ 545.32	281.35 $\pm$ 537.34
Internode elongation	128.30 $\pm$ 175.44	84.28 $\pm$ 142.09

active than dead buds on all sampling dates, and numbers of dead buds were similar. Peláez *et al.* (1997) also found no differences in numbers of dead buds at the stem bases of *J. ichu*, *N. tenuis* and *P. napostaense* after controlled fires. These results suggest that fire and defoliation affect the three species in similar ways. However, Peláez *et al.* (2009) found a lower number of dead buds in *P. ligularis* than in *P. napostaense* after burnt plants were defoliated during the vegetative stage. These results suggest that bud viability in these species could be affected by the length of the resting period after burning. If this period is short and defoliation occurs during the vegetative stage, tiller production might decrease.

Regarding the second part of the third hypothesis, we confirmed that the numbers of all and metabolically active bud were lower on tillers of *P. ligularis* than on tillers of *A. ambigua* and *N. tenuis*. The greater basal area and total number of tillers at the time of burning in *P. ligularis* ( $146.7 \pm 60.2$  cm<sup>2</sup> basal area,  $391.3 \pm 181.7$  tillers; mean  $\pm$  SD,  $n = 6$ ) than in *A. ambigua* ( $47.6 \pm 60.2$  cm<sup>2</sup> basal area,  $117.3 \pm 74.2$  tillers; mean  $\pm$  SD,  $n = 6$ ) and in *N. tenuis* ( $40.3 \pm 60.2$  cm<sup>2</sup> basal area,  $123.3 \pm 74.2$  tillers; mean  $\pm$  SD,  $n = 6$ ) might have been a reason for more intense burning of *P. ligularis* than the other two species. Because of that, higher temperatures at the growing points of *P. ligularis* could have affected to a greater extent its axillary buds. However, greater numbers (mean  $\pm$  SD,  $n = 96$ ) of green tillers in plants of this species (*P. ligularis*:  $281.17 \pm 282.1$ , *A. ambigua*:  $125.59 \pm 91.5$ , *N. tenuis*:  $101.73 \pm 98.6$ ;  $F_{2,285} = 27.99$ ,  $p < 0.0001$ ) suggests that even though *P. ligularis* has the lower number of buds per tiller, its persistence and productivity in grasslands would not suffer as a result of burning and/or successive defoliations. *Poa ligularis* has, therefore, greater numbers of total and metabolically active axillary buds than the two other study species, which promotes the increase in the above-ground biomass production in this species (cf. also Ithurrart *et al.* 2017). These properties confer an important competitive advantage to *P. ligularis* in comparison with the other two species.

The measurements in this study were conducted at an individual tiller scale. However, individual tillers, in addition to be autonomous

within the plant, are interconnected (Briske & Richards 1995), so it is expected that the differences shown among species are typical to entire plants rather than to their particular tillers.

## Conclusions

The study species were well adapted to the applied disturbance levels. Moderate defoliation after fire did not compromise the growth or survival of these in temperate, semiarid rangelands of central Argentina. Further research should determine the threshold above which burning (timing, intensity, etc.) followed by defoliation (timing post-burning, intensity, frequency, etc.) become limiting factors for the survival and productivity of the desirable species, under the local edapho-climatic conditions.

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