

Total Soil Available Nitrogen under Perennial Grasses after Burning and Defoliation¹

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Abstract—Total soil available nitrogen concentrations ($\text{NO}^{-3} + \text{NH}_4^{+}$) were determined underneath plants of the more-competitive *Poa ligularis*, mid-competitive *Nassella tenuis* and the less-competitive *Amelichloa ambigua* exposed to various combinations of controlled burning and defoliation treatments. Defoliations were at the vegetative (V), internode elongation (E) or both developmental morphology stages (V + E) during two years after burning in northeastern Patagonia, Argentina. Hypotheses were that (1) concentrations of total soil available nitrogen after burning are greater underneath burned than unburned plants. With time, these differences, however, will gradually disappear; (2) greater total soil available nitrogen concentrations are underneath plants of the more- than less-competitive perennial grasses; and (3) total soil available nitrogen is similar or lower underneath plants defoliated at the various developmental morphology stages in all three study species than on untreated controls at the end of the study. Concentration of total soil available nitrogen increased 35% ($p < 0.05$) on average after the first six months from burning in comparison to control plants. However, these differences disappeared ($p > 0.05$) towards the end of the first study year. Total soil available nitrogen concentrations were at least 10% lower underneath the less competitive *N. tenuis* and *A. ambigua* than the more competitive *P. ligularis* on average for all treatments, although differences were not significant ($p > 0.05$) most of the times. Defoliation had practically no effect on the concentration of total soil available nitrogen. Rather than any treatment effect, total soil nitrogen concentrations were determined by their temporal dynamics in the control and after the experimental fire treatments.

Keywords: fire, defoliation, ammonium, nitrate, grasses

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INTRODUCTION

The industry of beef livestock production in Argentina is mostly based on grazing of native vegetation of arid and semiarid rangelands which cover approximately 75% of the continental territory (Fernández and Busso, 1999). These rangelands are exposed to various, interacting biotic (e.g., grazing) and abiotic (e.g., fire, drought) factors which contribute to determine their current and future species composition (Anderson, 1984). At the same time, these factors might produce changes in the distribution, growth and survival of vegetation, and the characteristics of the microenvironment where it develops (Anderson, 1983). While droughts are completely unpredictable

events, fire and grazing are disturbances which can be managed by human beings. This is because it is important to study their dynamics, their interaction with the surrounding environment (climate, soil, microorganisms, etc.) and their consequences on the species in the plant community (Anderson, 1984). Thus, these disturbances which could cause considerable damage under natural conditions and even death of various perennial grass species (Bogen et al., 2003), could be used as management tools for the improvement of rangelands allowing to increase the efficiency of these production systems.

Studies conducted on different world ecosystems demonstrate that the effects of fire on soils are variable. It depends on the (1) severity, (2) quality, (3) degree of ash incorporation into the soil, and

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(4) frequency of fires (Arocena and Opio, 2003; Hubbert et al., 2006). The combination of the maximum temperature and exposure time reached during burning produce a thermic impact on the soil. It also depends of its water content and texture both of which influence the heat transmission into the soil (Hepper et al., 2008). Even though soil nutrient losses through the volatilization and lixiviation processes occur during burning (Giardina et al., 2000), increments in total soil available nitrogen and other nutrients in the short-term have been reported as a result of the soil organic matter mineralization and the ash left by the aboveground biomass (Daubenmire, 1968; Albanesi and Anriquez, 2003).

Nitrogen is one of the nutrients which most limit net primary productivity of natural ecosystems, mainly in arid or semiarid areas (Fenn et al., 1998). Plants are involved in the nitrogen cycling of ecosystems because of they (1) absorb the total soil available nitrogen (ammonium + nitrate), and (2) assimilate it and produce biomass, which will eventually decompose and release nitrogen (Raison, 1979). Plant species differ in nitrogen uptake rates, litter quality and the efficiency for producing biomass per unit nitrogen investment, thus distinctly affecting plant decomposition and nitrogen cycling (Knops et al., 2002; Saint Pierre et al., 2002). For example, nitrogen uptake rates and litter quality (e.g., more N content) have been reported to be greater on more- than less-competitive species (Saint Pierre et al., 2002). It is then expected that total soil available nitrogen (e.g., nitrate, ammonium) is greater underneath the canopy of more- than less-competitive species.

Hoglund (1985) reported that loses of soil nitrogen were greater on hard than laxly sheep grazed treatments on a dayland ryegrass-white clover pasture in New Zealand. This author emphasized the importance of allowing some litter cycling by avoiding continual hard grazing. In agreement with these results, Li et al. (2011) showed that total soil available nitrogen was significant lower on lightly than severely grazed Tibetan alpine meadows partly dominated by perennial grasses. In comparison to controls, grazing of the perennial grass *Piptochaetium napostaense* reduced levels of soil nitrate, but not those of ammonium, on upland grassland sites in Central Argentina (Harris et al., 2007). Ritchie et al. (1998) found that herbivory also decrease soil nitrate and total available nitrogen concentrations in an oak savanna. Selective herbivory (e.g., domestic animals) can reduce the rate of nutrient cycling by changing the species composition from high nutritional quality, palatable to low nutritional quality, unpalatable species (Anderson et al., 2007). In spite of this, Semmartin et al. (2006) did not find significant differences in nitrogen dynamics between grazed and ungrazed sites after making continuous measurements on grasslands in Uruguay.

The effects of fire with or without defoliation at different developmental morphology stages have not yet been quantified on the autoecology of the highly competitive, palatable *P. ligularis* (Distel and Bóo, 1996; Cano, 1988), the intermediate-competitive, palatable *N. tenuis* (Cano, 1988; Saint Pierre et al., 2002) and less-competitive, unpalatable *A. ambigua* (Cano, 1988; Saint Pierre et al., 2004a, 2004b). These species are abundant in rangelands of central Argentina (Fernández and Busso, 1999), although this abundance depends at least partially on the relative effects of fire with or without grazing, and of domestic livestock management (Distel and Bóo, 1996). This information is critical for conducting a more appropriate management of *N. tenuis* and *P. ligularis*, which constitute an important forage resource in the arid and semiarid areas of the Monte of Argentina. Our objective was to determine the total soil available nitrogen concentration ($\text{NO}_3^- + \text{NH}_4^+$) underneath plants of *P. ligularis*, *N. tenuis* and *A. ambigua* exposed to various combinations of controlled burning and defoliation at the vegetative, internode elongation or both developmental morphology stages during a year and a half after burning. Working hypothesis were that (1) the concentration of total soil available nitrogen immediately after burning is greater underneath burned than unburned plants. With time, these differences, however, will gradually disappear; (2) greater total soil available nitrogen concentrations at the end of the study are underneath plants of more- (e.g., *P. ligularis*) than less-competitive (e.g., *N. tenuis*) perennial grass species; and (3) total soil available nitrogen is similar or lower, but not greater, underneath plants defoliated at the different study developmental morphology stages in all three study species than on undefoliated controls at the end of the study.

MATERIALS AND METHODS

Study Site

This study was conducted within a 15-year-exclosure to domestic livestock in the Chacra Experimental Patagones, southwest of the Province of Buenos Aires (40°39'49.7" S, 62°53'6.4" W; 40 m a.s.l.; Fig. 1), within the Phytogeographical Province of the Monte during 2011 and 2012 (Cabrera, 1976).

Climate

It is temperate semi-arid, with precipitations concentrated in summer and autumn. Precipitation, air and soil temperatures and relative humidity were provided by a meteorological station located 1 km away from the study area. Total annual precipitation was 444 mm during 2011, and 513 mm during 2012. Annual mean precipitation was 421 mm during 1981–2012 with minimum and maximum values of 196 mm (2009) and 877 mm (1984), respectively (Ing. Monte-

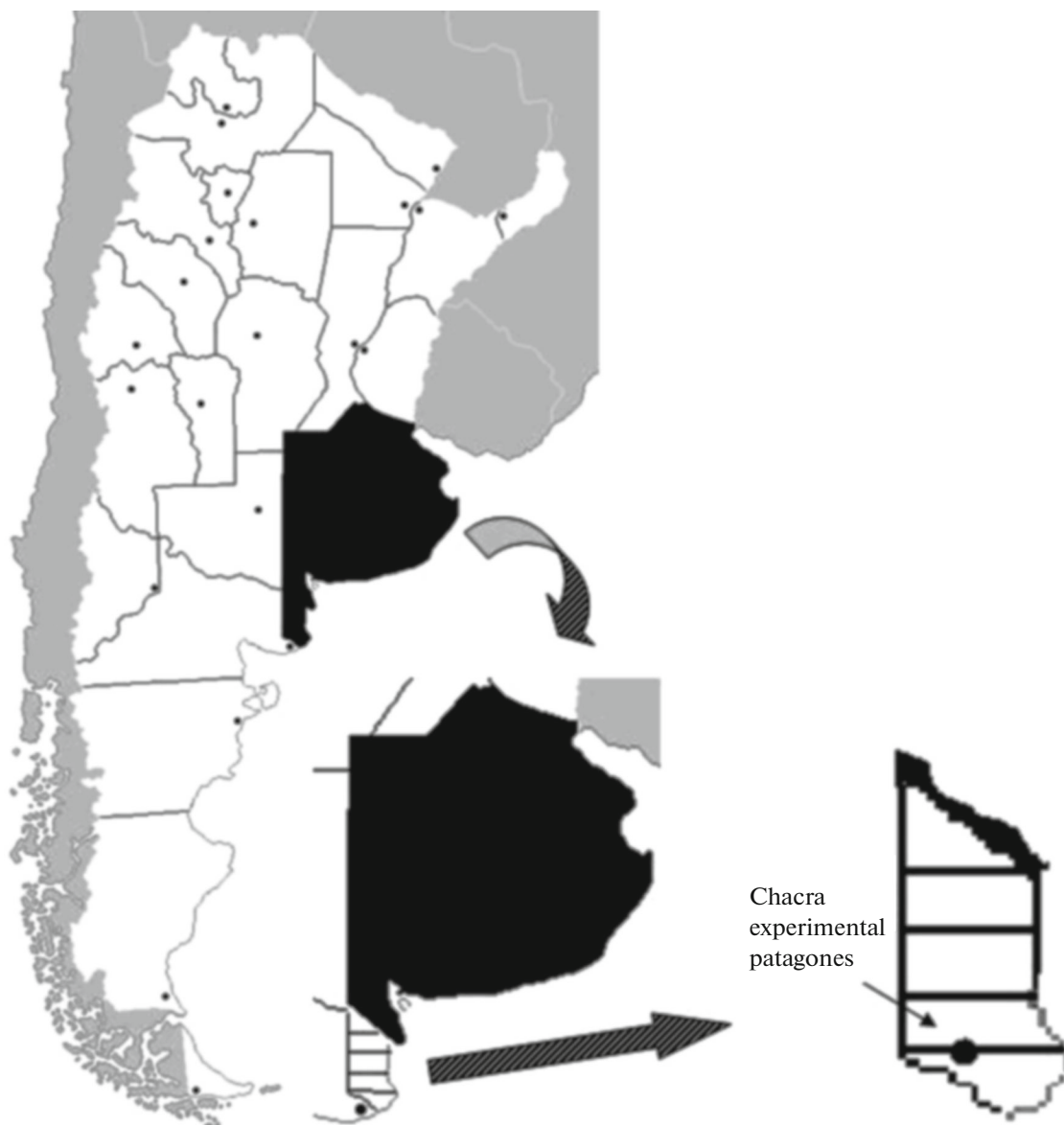


Fig. 1. Location of the study site: Chacra Experimental Patagones, Ministerio de Asuntos Agrarios, Province of Buenos Aires, Argentina.

negro, Chacra Experimental Patagones, Ministerio de Asuntos Agrarios de la Provincia de Bs. As., personal communication). Mean annual air temperatures were 15°C during both 2011 and 2012. Mean monthly maximum soil temperatures (January = summer) were 23.1°C during 2011, and 24.6°C during 2012. During these years, mean monthly minimum soil temperatures (July = winter) were 6.2°C in 2011 and 3.9°C in 2012. Long-term (1981–2012) mean monthly maximum relative humidity was 77.9% in July and 55.1% in December (late spring–early summer).

Soil

Landscape on the region is mostly a plain although there are waves and isolated microdepressions. The

original materials of the predominant soils are fine sands, which are transported by the wind and deposited on tosca, and loamy-sandy, weakly consolidated older materials (INTA-CIRN, 1989). Soil was classified as a typical Haplocalcid in the Chacra Experimental de Patagones (Nilda Mabel Amiotti, Dpto. de Agronomía UNSur, personal communication). Mean pH is 7 and there are no limitations of depth in the soil profile.

Vegetation

The plant community is an open shrubby stratum that includes herbaceous species of different quality for livestock production (Giorgetti et al., 1997). *Poa ligularis* Ness. (a high competitive species: Distel and

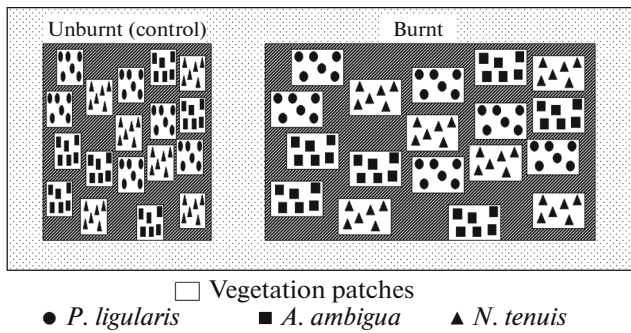


Fig. 2. Schematic diagram of the used experimental design. Plots of the three species ($n = 6$; i.e., $3 \times 6 = 18$) are included in the diagram per treatment under the Burned Area Heading (i.e., 18×5 burning with or without defoliation treatments = 90 plots; see Table 1). Unburned and undefoliated plots (Control Heading) of the three species (i.e., $18 = 3 \times 6$) plus 90 plots = 108 plots were used in the whole study.

Bóo, 1996), *Nassella tenuis* (Phil.) Barkworth (an intermediate-competitive species: Saint Pierre et al., 2002) and *Amelichloa ambigua* (Speg.) Arriaga and Barkworth (a low competitive species: Saint Pierre et al., 2002) are three C_3 native perennial grasses in the Phytogeographical Province of the Monte, Argentina. This Province includes approximately 554,138 ha in the Partido de Patagones, Province of Buenos Aires. Dominance of these species in the community depends, at least in part, of the grazing history and frequency and intensity of fires (Distel and Bóo, 1996). Characteristic rangeland management at the south of this region is continuous grazing with excessive stocking rate (Bóo and Peláez, 1991). *Amelichloa ambigua* has a low preference by grazing animals (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*, might be highly selected by domestic herbivory at different times during their morphological development after accidental fires.

Experimental Design

We followed a completely randomized experimental design with balanced replicates ($n = 6$). Analyzed

factors were the (1) species, (2) treatments and (3) sampling dates.

Thirty six vegetation patches (1 m² each) were selected for each of the study species at the study site [*P. ligularis*, *N. tenuis* and *A. ambigua*]; 36×3 species = 108 patches]. Six replicate patches were used per treatment and plant species (6 treatments \times 3 species/treatment \times 6 replicates/species/treatment = 108 patches). Each vegetation patch, which contained at least 6 plants of any of the study species, constituted an experimental unit (Fig. 2). Out of the 108 patches, 90 were burned and either (1) not defoliated or (2) defoliated during the first or second or both study years after the controlled burning (Table 1, Fig. 2). The 18 remaining, unburned patches were not defoliated and used as a control (Fig. 2).

Controlled Burning

The mean climatic conditions during burning (from 12:30 to 1:00 PM) were: 21.8–22.4°C air temperature, 28% air relative humidity, and 19.3–20 km/h wind speed (wind direction: NW – WNW). Soil moisture content was $5 \pm 0.4\%$ (mean \pm 1 S.E., $n = 14$). Fine fuel accumulation was 3.887.6 kg dry matter/ha; it had a $9.1 \pm 1.5\%$ plant tissue moisture (mean \pm 1 S.E., $n = 10$). Maximum soil surface temperature was 560°C (Fig. 3).

Treatments

Each treatment consisted of a combination of burning, either without or with defoliation at the vegetative or internode elongation or both developmental morphology stages during the first (2011) or second (2012) or both study years. Vegetation patches neither burned nor defoliated were used as a control (Table 1).

Controlled burnings in the study region are often conducted towards the end of summer-early fall to favor growth of the species which grow in fall, winter and spring. The controlled, experimental burning was conducted on 23 March 2011 in an area that included 108 patches (Fig. 2). Prior to burning, the amount of fine fuel was determined [i.e., plant material over the soil surface (including litter) of a diameter less than or equal to 3 mm]. This plant material was first collected

Table 1. Detail of treatments applied to vegetation patches ($n = 6$) of more (e.g. *P. ligularis*), intermediate- (e.g., *N. tenuis*), and early-successional stage species (e.g., *A. ambigua*) during 2011 and 2012. UB—unburned; B—burned; UD—un-defoliated; DV—defoliated at the vegetative (V) stage; DE—defoliated at the internode elongation (E) stage; D (V + E)—defoliated at the vegetative and internode elongation stages

Treatments	At the beginning of the study	During 2011	During 2012
1 (control)	UB	UD	UD
2	B	UD	UD
3	B	DV	DV
4	B	DE	UD
5	B	D (V + E)	DV
6	B	UD	DV

using 10 quadrats of 1m² each and then dried in an oven (72 h at 72°C). Soil moisture was determined gravimetrically in the top 5cm soil depth following Brown (1995). Temperatures during burning were measured with 8 type-K (chromel-alumel) thermocouples at 1 second-intervals. They were located at the soil surface level, without touching the soil, in areas with different fine-fuel accumulation (high, intermediate, low) (Bóo et al., 1996). Temperature, however, was an integrative, mean determination measured by those 8 thermocouples from areas with different fine fuel loads. Temperatures were registered connecting the thermocouples to a datalogger (Campbell 21 XL) which was buried approximately to 1 m soil depth. Field instruments were used to measure wind speed, air temperature and relative humidity at the burning time. Another area was left unburned (i.e., control).

Defoliations were conducted to 5 cm stubble height from the soil surface at various developmental morphology stages. These stages were either (1) vegetative (15/08/2011 and 06/05/2012) or (2) during internode elongation (14/10/2011 and 14/09/2012) or (3) vegetative + internode elongation. At the end of each growing cycle (06/01/2012 and 20/12/2012), plants were defoliated once again to 5 cm stubble height to obtain the total plant biomass production. After each defoliation, the plant material was oven-dried to 72°C during 72 h and weighed. Neighboring plants were also burned and/or defoliated similarly to those measured to provide of a uniform competitive environment.

Sampling Procedures

After burning, samplings were conducted on 04/04/11, 11/05/11, 30/09/11, 03/12/11 and 05/06/12 to determine total soil available nitrogen. On each sampling date, a soil sample (500 g) was obtained from the periphery of each plant ($n = 6$) at 5 cm soil depth using an auger. Nitrogen was determined in the soil as N-NH₄⁺ and N-NO₃⁻ following Mulvaney et al. (1996). Such values were added to obtain total soil available nitrogen.

Statistical Analysis

Data were analyzed using the statistical software INFOSTAT (Di Rienzo et al., 2013). Previous to analyses, data were transformed to $\ln(x + 1)$ for shoot dry weight to comply with the assumptions of normality and homocedasticity (Soakal and Rolf, 1984). Untransformed values are shown in Figures and Tables. Shoot dry weight per plant was analyzed using two-way ANOVA, taken species and treatments as factors. In the case of total soil available nitrogen, and because the number of treatments differed among sampling dates, a table of double entrance was conducted using a two-way ANOVA (species \times treatments) for each sampling date, and a two-way ANOVA (species \times sampling date) for each treatment; when interactions were

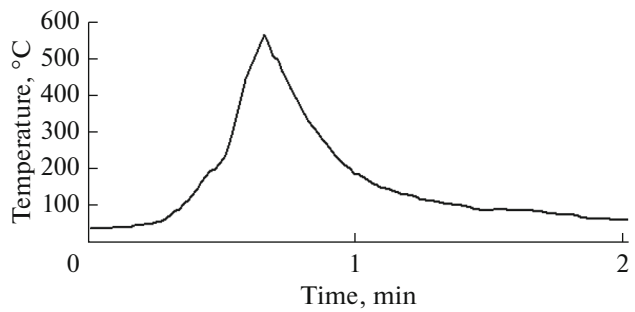


Fig. 3. Mean temperatures reached during burning during a 2-minute-period. Temperatures were taken using a 1-second-interval among measurements. Each data on the curve is the mean of $n = 8$ thermocouples.

found, one-way ANOVAs were conducted for each factor separately. Mean comparisons were made using the Tukey's test with a significance level of 0.05.

RESULTS

Shoot Dry Weight Per Plant

No significant interaction ($p > 0.05$) was detected between species and treatments, and no differences ($p > 0.05$) were found among treatments (Table 2). At the end of two growing cycles, plants of *P. ligularis* and *A. ambigua* produced a greater dry biomass ($p \leq 0.05$) than those of *N. tenuis* (Fig. 4). Differences between *P. ligularis* and *A. ambigua*, however, were not significant ($p > 0.05$).

Total Soil Available Nitrogen

Twelve days after burning, total soil available nitrogen below the canopy of the study species was similar ($P > 0.05$) on burned than on unburned sites; total soil available nitrogen was greater ($P \leq 0.05$) below the canopy of *A. ambigua* than that found below the canopy of the desirable perennial grasses (Fig. 5). In the two following sampling dates, there was more ($P \leq 0.05$) total soil available nitrogen in the burned than in the unburned sites (Fig. 5). At the second sampling date, however, no differences ($P > 0.05$) among species were found (Fig. 5). Soil underneath the canopy of *A. ambigua* and *P. ligularis* showed greater ($P \leq 0.05$) available nitrogen concentration than underneath that of *N. tenuis* at the third sampling date. In December 2011, soil underneath the canopy of *A. ambigua* showed a greater ($P \leq 0.05$) concentration of available nitrogen when plants of this species were exposed to T2 than T5. At the same time, no differences ($P > 0.05$) were detected among treatments in the total soil available nitrogen concentration underneath the plants of the palatable species. Soil samples underneath *A. ambigua* exhibited greater ($P \leq 0.05$) available nitrogen concentrations than those underneath *S. tenuis* in T2 and T3. Finally, in June 2012, soil nitrogen concentrations were greater ($P \leq 0.05$) in the

Table 2. Results of a two-way analysis of variance examining the effects of plant species and defoliation treatments on aboveground biomass production (g dry weight/plant) of *Poa ligularis*, *Nassella tenuis* and *Amelichloa ambigua* after a controlled fire (see Table 1) in a semiarid region in the Chacra Experimental of Patagones, Buenos Aires, Argentina. Data are presented in Fig. 4

Mean sums of squares and significance level		
<i>df</i>	aboveground biomass (g dry weight/plant)	
Source		
Model	23	55.49****
Species	2	40.26****
Treatments	7	4.89
Species × Treatments	14	10.33
Error	120	58.54
Total	143	114.02

**** $P < 0.0001$.

control than in T2 (underneath *P. ligularis*) and T5 (underneath *A. ambigua*); at the same time, soil nitrogen concentrations underneath *N. tenuis* were similar ($P > 0.05$) in all treatments (Fig. 5). However, total soil available nitrogen concentrations were lower ($P \leq 0.05$) underneath *N. tenuis* than *P. ligularis* (in the control, T3 and T4) and *A. ambigua* (in T6); simultaneously, there were no differences ($P \leq 0.05$) among species in T2 and T5 (Fig. 5).

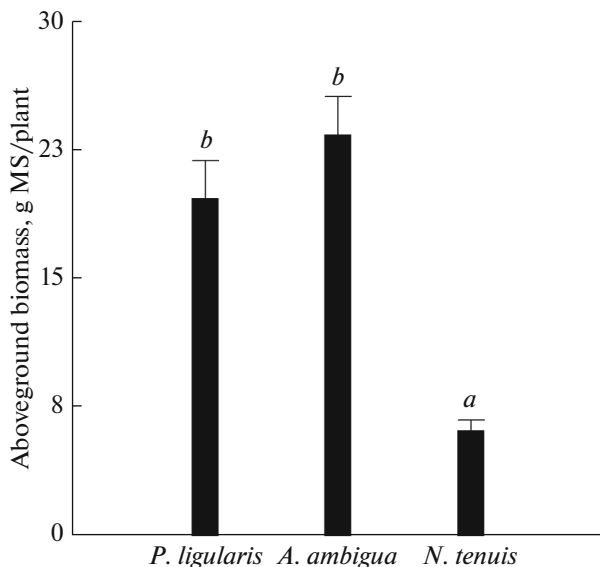


Fig. 4. Aboveground biomass (g/plant) of *P. ligularis*, *N. tenuis*, or *A. ambigua* either exposed or not to various controlled burning and defoliation treatments (see Table 1). Each histogram is the mean \pm 1 standard error of $n = 48$. Different letters above histograms indicate significant differences ($p \leq 0.05$) among species.

Total soil available nitrogen concentrations increased ($P < 0.05$) between 2 to 4 times from the first to the last sampling date in all species in the control treatment (Table 3). In the burning with or without defoliation treatments, such concentrations increased ($P < 0.05$) from 1.2 to 3.6 times in 11 out of 12 comparisons from any previous to the last sampling time (i.e., December 2012) in all species (Table 3). The exceptions occurred in the T2 treatment at the end of September 2011 in all three species, and in *N. tenuis* in the T4 treatment on early December 2011 (Table 3). There was an increase ($P \leq 0.05$) in available soil nitrogen concentrations from mid-May to late September 2011 in the Control and T2 treatments on all three species; differences, however, were not significant ($P > 0.05$) on *P. ligularis* in the control treatment (Table 3). From the end of September to early December 2011, there was a decrease ($P \leq 0.05$) in available soil nitrogen concentrations in T2 and T3 on all three species (Table 3).

DISCUSSION

Controlled Burning

The shape of the time-temperature curve seems to be typical of grassland fires (Bóo et al., 1996). Maximum temperature reached with the moderately severe fire was similar to that reported for other rangeland, controlled fires conducted under similar abiotic conditions (i.e., climate, soil and plant moisture contents) with similar fine fuel loads (Bóo et al., 1996). These authors emphasized that the effect of repeated moderately severe fires combined with proper grazing might be the key factor to reduce undesirable perennial grass species and improve grazing in rangelands of central Argentina.

Shoot Dry Weight Per Plant

Poa ligularis, *N. tenuis* and *A. ambigua* showed a similar biomass production in all study treatments. These results of a similar biomass production between plants exposed to defoliation with or without a controlled burning are supported by postfire clipping trials conducted by Bunting et al. (1998) and Jirik and Bunting (1994). In their work, severe defoliation by a single clipping of individual bunchgrasses after seed development did not affect yield the following year on various perennial grass species when compared with undefoliated plants. Bates et al. (2009) also reported that annual yield of the perennial grass group was similar between summer-grazed and ungrazed burn treatments. In addition, these authors reported that annual yield after spring grazing did not differ among the burn and burn-grazed treatments. Our results indicate that properly applied defoliation treatments following fire will not reduce the recovery of the study perennial grasses. Nevertheless, the results and interpretation of this study must be considered under the conditions it was conducted. This is because the study was con-

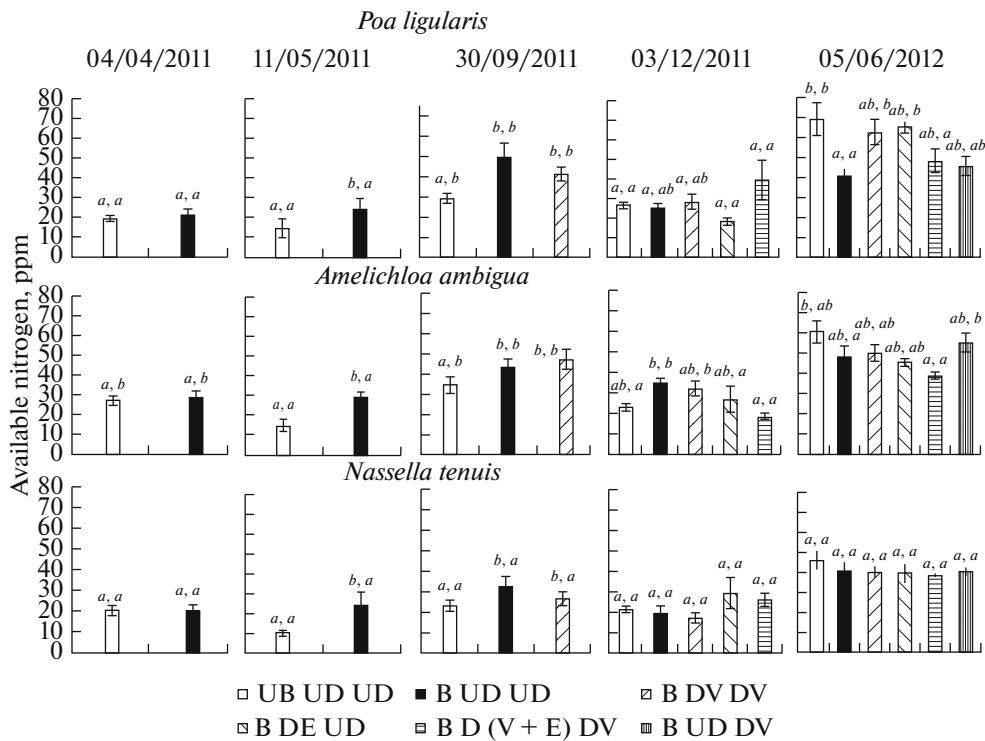


Fig. 5. Total total soil available nitrogen ($\text{N-NH}_4^+ + \text{N-NO}_3^-$; ppm) underneath plants of the more-competitive *P. ligularis*, the intermediate-competitive *N. tenuis*, and the early-competitive *A. ambigua* either exposed or not to various controlled burning and defoliation treatments (see Table 1). Each histogram is the mean \pm 1 standard error of $n = 6$. Different letters before the comma indicate significant differences ($p \leq 0.05$) among treatments. Different letters after the comma indicate significant differences ($p \leq 0.05$) among species.

ducted at a plant scale, with fires causing minimal, if any, mortality to the study perennial grasses, with strictly controlled defoliation protocols. Whenever one or more of these elements vary in other situations, it will generate a host of postfire recovery scenarios. The greater biomass production in *P. ligularis* than in *N. tenuis* can be attributed to the greater competitive ability (Saint Pierre et al., 2002; Saint Pierre et al., 2004a), and the greater tiller number and size (Ithurrtart, 2015) on plants of the first than the second species. Ithurrtart (2015) reported an at least 48% greater total tiller number on plants of *P. ligularis* than on those of *A. ambigua*, although this last species showed a greater tiller size [total leaf length (blades + sheaths, dry + green leaves)/tiller; overall mean for all treatments and sampling dates: *A. ambigua* = 23.4 ± 3.6 cm; *P. ligularis* = 20.0 ± 2.3 cm] than *P. ligularis*. This contributes to explain the similar dry biomass production on plants of *P. ligularis* and *A. ambigua*.

Total Soil Available Nitrogen

Differences in soil available nitrogen concentrations underneath plants of all three study species were smaller than those in the aboveground plant biomasses of these species. These results agree with those of Saint

Pierre et al. (2004c). These authors also found that the differences in soil phosphorus concentrations under plants of *Nassella clarazii*, *N. tenuis* and *A. ambigua* were smaller than the differences in their aboveground plant biomasses. This might be related to the myriad of factors which affect the available concentrations of nutrients in the soil (Comerford, 2005).

Ambrosino et al. (2014a) found that roots from plants of *A. ambigua* supplied a greater amount of organic matter to the soil than those of *P. ligularis* and *N. tenuis* after a two-month-period at the same study site. This might help to explain that the concentration of total soil available nitrogen was initially greater underneath plants of *A. ambigua* than below the canopy of the other study species. Sampling was conducted on the shallower soil surface layers in the fall 2011. Celaya Michel and Castellanos Villegas (2011) showed that the greater amount of organic matter for decomposition and mineralization processes is in the first centimeters of soil.

There was not an immediate increase in total soil available nitrogen after burning. Burning of grasslands can yield immediate increases in inorganic nitrogen as a result of the physicochemical decomposition of the organic matter because of heat (Kovacic et al., 1986). However, this increase can be compensated by the

Table 3. Variation through time on the available nitrogen concentrations (N-NH₄⁺ + N-NO₃⁻; ppm) underneath plants of *P. ligularis*, *N. tenuis* y *A. ambigua* either exposed or not to various controlled burning and defoliation treatments (see Table 1)

Treatments	Species	04/04/2011	11/05/2011	30/09/2011	03/12/2011	05/06/2012
T1 (control)	<i>A. ambigua</i>	27.07 ¹ ± 2.18 ² ab ³	15.27 ± 3.05a	34.51 ± 3.95b	22.77 ± 1.69ab	60.44 ± 5.64c
	<i>N. tenuis</i>	20.58 ± 2.47ab	10.30 ± 1.46a	23.16 ± 2.80b	21.38 ± 1.28ab	43.80 ± 4.30c
	<i>P. ligularis</i>	17.22 ± 1.30a	14.52 ± 4.96a	29.36 ± 2.32a	26.49 ± 1.52a	69.32 ± 8.14b
T2	<i>A. ambigua</i>	29.73 ± 2.33a	29.18 ± 3.15a	43.14 ± 4.08b	34.44 ± 2.64a	48.09 ± 5.11b
	<i>N. tenuis</i>	20.92 ± 2.24a	27.22 ± 3.70a	32.51 ± 5.08b	19.45 ± 3.62a	39.51 ± 3.24b
	<i>P. ligularis</i>	20.92 ± 3.09a	23.93 ± 6.12a	49.36 ± 7.20b	24.94 ± 2.61a	40.23 ± 6.35b
T3	<i>A. ambigua</i>	—	—	47.30 ± 5.01b	32.14 ± 3.61a	50.10 ± 3.94c
	<i>N. tenuis</i>	—	—	26.74 ± 3.16b	17.43 ± 2.41a	38.05 ± 2.80c
	<i>P. ligularis</i>	—	—	41.23 ± 3.20b	28.38 ± 3.79a	62.68 ± 6.54c
T4	<i>A. ambigua</i>	—	—	—	27.24 ± 6.24a	45.39 ± 1.82b
	<i>N. tenuis</i>	—	—	—	29.64 ± 7.88a	37.72 ± 4.16a
	<i>P. ligularis</i>	—	—	—	18.21 ± 1.67a	65.60 ± 3.28b
T5	<i>A. ambigua</i>	—	—	—	18.62 ± 1.38a	38.69 ± 1.86b
	<i>N. tenuis</i>	—	—	—	26.21 ± 3.02a	36.68 ± 1.09b
	<i>P. ligularis</i>	—	—	—	39.51 ± 10.2a	48.17 ± 5.76b
T6	<i>A. ambigua</i>	—	—	—	—	55.13 ± 4.64
	<i>N. tenuis</i>	—	—	—	—	38.75 ± 1.86
	<i>P. ligularis</i>	—	—	—	—	45.55 ± 4.82

¹ Available soil N (ppm). ² Each value is the mean ± 1 standard error of $n = 6$. ³ Means with different letters in the same row indicate significant differences ($p \leq 0.05$) among sampling dates according to the Tukey's test.

immediate nitrogen losses that occur in the soil during burning as a result of fuel combustion (Blair, 1997). In addition, the high temperatures reached in the more superficial soil layers after burning can determine an immediate reduction in the number of soil microorganisms responsible of the organic matter decomposition (Ahlgren and Ahlgren, 1965). Because of this, initial differences between burned and unburned sites might not be detected. However, thereafter, and in agreement with the first hypothesis, inorganic nitrogen releases through nitrification processes can increase the amounts of total soil available nitrogen beyond levels found in unburned areas (DeBano et al., 1998). This effect of fire was conspicuous six weeks after the occurrence of such disturbance, and kept increasing until the end of September. Even though it is possible a decrease in the number of microorganisms immediately after burning, the heat and ashes can modify the chemical soil properties contributing to its recuperation until reaching levels much higher than those found on unburned soils (Ahlgren and Ahlgren, 1965). On the other hand, some authors report that the ash increases coming from burning of grasslands dominated by herbaceous species is low, and insufficient to cause detectable changes in the pH or nutrient availability (Raison, 1979). Fire might make soil more favorable to bacteria than fungi, possibly because of the increases of the soil pH and soluble sugars in the

soil solution (Raison, 1979). Renbuss et al. (1973) mentioned that after an initial reduction immediately after fire, the number of nitrifying bacteria returned to normality within a week, increased ten times after a month, and reached its maximum level after 18 weeks. However, such number returned to its initial values after 48 weeks (Renbuss et al., 1973). Thereafter, alterations in the amount of ammonium in the soil, soil pH, temperature and microbial activity might contribute to increase nitrification rates of soil nitrogen even more after fire (Raison, 1979).

At the end of the first (2011) growing cycle, there were no significant differences in the concentration of total soil available nitrogen between the burned and unburned treatments. Picone et al. (2003) showed that the increase in the nitrogen concentration after burning can be transitory because, at least in part, it is susceptible of having different losses in the soil. Other authors reported that the high ammonium levels in the soil generally persist during some months and then decline to reach the initial nitrogen levels one year after burning (DeBano et al., 1998). The decline is mostly due to nitrogen losses because of the processes of nitrification, lixiviation, microbial immobilization and plant nitrogen uptake (DeBano et al., 1998). Wan et al. (2001) additionally mentioned that there exists a differential response between the soil ammonium and

nitrate. Immediately after burning, the soil ammonium content is twice as much, and then there is a gradual decline up to reaching the initial values after a year (Wan et al., 2001). On the other hand, nitrate increase is small immediately after burning, values can be three times as much after six and twelve months from burning, and a nitrate decline can be observed afterwards (Wan et al., 2001). This contributes to explain our results at the end of the first study year.

Overall, increases in total soil available nitrogen concentrations in controls at the last sampling date were often at least twice as much as those in the burning with or without defoliation treatments. This indicates that concentrations of total soil available nitrogen on untreated plants were greater than any study treatment effect at this time. Highest concentrations at the last sampling date in all treatments were most likely related to the greater plant size at that time. At the last sampling date (i.e., June, 2012), the number of total (dead + alive) tillers per plant had increased ($P < 0.05$), with respect to numbers at the study initiation, from 139.8 ± 22.0 to 442.4 ± 49.9 in *P. ligularis*; 86.2 ± 8.7 to 165.8 ± 23.2 in *N. tenuis*, and 15.2 ± 6.2 to 260.7 ± 23.9 in *A. ambigua* (Ithurrart, 2015). At the same time, values of root length density (cm root/cm³ soil) increased ($P < 0.05$) from 1.35 ± 0.06 to 1.98 ± 0.04 from the first (11 May, 2011) to the last (18 October, 2012) sampling date, respectively, on average for all treatments and species (Ithurrart, 2015). Roots are an important source of material of easy decomposition because of the microbial activity on rangelands dominated by perennial grasses, where biomass is greater below- than aboveground in most plants (Coleman et al., 1983). An increased amount of plant residues in the soil usually increase the levels of total soil available nitrogen, and very likely of potentially mineralizable nitrogen (https://www.nrcs.usda.gov/wps/PA_NRCSCconsumption/download?cid=stelprdb124337&ext=pdf). In addition, low growth of these C₃ species during winter (Busso et al., 2003; Saint Pierre et al., 2004c) might reduce plant nitrogen demands, and subsequently increase levels of available nitrogen in the soil. Li et al. (2011) determined that low shoot growth led to increases in total soil available nitrogen as a result of increased grazing intensity in the Tibetan Plateau.

Moretto and Distel (2002, 2003) reported that litter of competitive, palatable perennial grasses showed high nitrogen concentrations, low carbon/nitrogen ratios and low lignin concentrations in semiarid rangelands; this resulted in a fast litter decomposition and nutrient mineralization. Low nutritive value species, however, produce litter more difficult to decompose (Aerts and De Caluwe, 1997). A parallel study at the study site than ours showed that *P. ligularis* produced a greater amount of leaf litter than *N. tenuis* during a growing cycle when these species were not exposed neither to burning nor defoliation (Ambrosino et al.,

2014b). Moretto and Distel (2003) found a greater mineralization rate on plants of the more competitive *P. ligularis* than on those of the perennial grass, less competitive *Jarava ichu*. At the last sampling date in our work, and in accordance with our second hypothesis, concentrations of soil inorganic nitrogen were higher underneath plants of the more competitive *P. ligularis* than on those of the less competitive *N. tenuis* in three out of six comparisons. The either equal or lower nitrogen concentrations under *N. tenuis* than in the other two study species were most likely determined by the smaller volumes of organic material under plants of *N. tenuis* in comparison to those under *P. ligularis* and *A. ambigua* (e.g., see results of Ambrosino et al., 2014b above and Fig. 4).

After 15 months from burning, total soil available nitrogen concentrations were similar or lower, but not greater, underneath burned, either defoliated or undefoliated plants (overall means for burning with or without defoliation: *P. ligularis* = 52.45 ppm; *N. tenuis* = 38.14 ppm; *A. ambigua* = 47.48 ppm) than on unburned controls (see Table 3). These results agree with our third hypothesis, and are similar to those reported by Wan et al. (2001). These authors showed that fire effects would result nearly imperceptible on soil nitrate or ammonium levels approximately after a year from burning. By reducing the abundance of nitrogen-rich grasses (e.g., *Poa ligularis*: Moretto and Distel, 2002; Sainte Pierre et al., 2004a) via selective grazing of the most palatable species, herbivores leave plant species that can significantly reduce the available nitrogen levels in the soil (Tilman and Wedin, 1991). Litter from these comparatively unpalatable plant species (low nitrogen concentrations, high C/N ratios: Moretto and Distel, 2002, 2003) often decompose slowly (e.g., *A. ambigua*: Ambrosino et al., 2014a), and may increase microbial uptake of N released from the litter of other plant species (Wedin and Pastor, 1993). Ritchie et al. (1998) reported that herbivore exclusion led to increased N mineralization rates. These authors suggested that the most likely explanation for the observed effects of herbivore exclusion on nitrogen availability appears to be the herbivore-induced changes in plant species composition that alter overall plant tissue nitrogen. After an 18 year-exclosure to any anthropic-induced disturbance, the less competitive, low-nitrogen-tissue *A. ambigua* (Saint Pierre et al., 2002) has been almost completely replaced by the more competitive, high-nitrogen-tissue *P. ligularis* and *N. clarazii* (Saint Pierre et al., 2002) (C.A. Busso, Departamento de Agronomía, Universidad Nacional del Sur, Bahía Blanca, Argentina, personal communication). The severe defoliations of the three species at the various developmental morphology stages after a controlled burning in our study determined either species-specific reductions at specific times or did not affect the total soil available nitrogen concentrations. However, we found that the total soil available nitrogen concentrations during the whole study were determined more by the temporal

dynamics of total soil available nitrogen in the control and after the experimental fire with or without defoliation treatments than by any treatment effect. However, Wan et al. (2001) emphasized that the plant cover elimination because of frequent and intense both fires and livestock grazing can affect ecosystem functioning in arid and semiarid zones, resulting in modifications that in the mid- or long-term could determine reductions in soil nitrogen content.

CONCLUSIONS

1. Differences in soil available nitrogen concentrations under plants of all study species were smaller than the differences in their aboveground biomasses.

2. Six months after burning, the total soil available nitrogen concentrations were more than 27% smaller on unburned than on burned, either defoliated or undefoliated areas. These differences most often disappeared after fifteen months from burning between unburned (overall mean \pm 1 S.E. for the three species = 57.8 ± 7.5 ppm) and burned with or without defoliation areas (overall mean for all treatments and species = 46.0 ± 5.3 ppm).

3. Total soil available nitrogen concentrations were more than 10% greater (although only occasionally significant at $p \leq 0.05$) underneath the more competitive *P. ligularis* than the less competitive *N. tenuis* and *A. ambigua* after fifteen months from burning in all treatments.

4. During the study, defoliation had practically no effect on the concentration of total soil available nitrogen in comparison with its temporal dynamics in the control and after the experimental fire with or without defoliation treatments.

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