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## Original article

# Fire and grazing in grasslands of the Argentine Caldenal: Effects on plant and soil carbon and nitrogen

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## ABSTRACT

Fire and grazing can modulate feedbacks between pools of carbon and nitrogen of plant and soil, altering cycles of these elements in grassland ecosystems. The magnitude of these effects may be limited by climate and by limited plasticity in tissue chemistry within a given photosynthetic pathway. We tested the hypotheses that (1) fire reduces rates of C and N cycling, while grazing increases them, and (2) these changes are due to intraspecific changes in plant tissue chemistry rather than competitive replacements by species with differing tissue chemistry. Plant and soil C and N content and isotopic ratios, soil microbial biomass C, and potential C mineralization were measured in areas of the southern Caldenal region of central Argentina with known histories of fire and grazing. Results support the hypothesis that fire reduces rates of N cycling via intraspecific increases in plant tissue C/N. Contrary to our first hypothesis, grazing also reduced plant tissue N. Fire and grazing effects on plant tissue chemistry resulted primarily from changes in dynamics of soil inorganic N. These changes were due to intraspecific changes in plant tissue chemistry, which was in agreement with our second hypothesis. Potential C mineralization experiments revealed little difference between treatments in pool sizes and mean residence times of labile soil organic carbon. Livestock grazing and fire have significant influences on soil N dynamics, particularly as mediated by soil microbes, in managed grasslands of the southern Caldenal in Argentina.

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## 1. Introduction

Cycles of carbon and nitrogen in terrestrial ecosystems are governed by dynamic feedbacks between vegetation and soils. In temperate grasslands, a rapidly cycling pool of soil organic matter (SOM) exerts a mediating influence on these feedbacks out of proportion to its small absolute mass. Thus, temperate

grasslands offer a high potential for the expression of disturbance effects, such as those caused by fire and grazing, on ecosystem C and N dynamics (Seastedt et al., 1994; Hobbs, 1996; Distel et al., 2005).

The C/N stoichiometry of plant biomass is both a product of and influence on the pool size, quality, and rate of flux of SOM (Hobbie, 1992). Changes in plant community structure

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and (or) plant tissue chemistry at the species level thus have the potential to alter belowground nutrient cycling processes, and vice versa. The influence of vegetation change on nutrient turnover may be disproportionately large or rapid due to the role of a small, labile pool of SOM in determining C and N dynamics (Wedin, 1995; Wedin and Tilman, 1996). However, climatic influences on productivity, decomposition, and mineralization are also important in determining pool sizes and fluxes of SOM (Post et al., 1982). This study examines the effects of prescribed fire and grazing on C and N pools in plants and soils of managed semiarid grasslands of Argentina.

In one conceptual model, fire and grazing induce positive feedback loops in plant-soil nutrient dynamics (Wedin, 1995; Wedin and Tilman, 1996). Following repeated burning, volatilization losses of N from aboveground biomass and increased N use efficiency lead to progressively higher C/N ratios in plant tissue and slower C and N turnover rates in soil pools (Ojima et al., 1994; Wan et al., 2001). Grazing, on the other hand, increases plant-available soil N via fecal returns (Ruess and McNaughton, 1987; McNaughton et al., 1988; Augustine et al., 2003), while reducing inputs of plant C to the soil. These alterations to C and N dynamics have the net effect of lowering plant C/N ratios and accelerating belowground turnover (Johnson and Matchett, 2001). This has been termed the ‘indeterminate dominance’ model due to the fact that in the mesic grasslands it describes, any one of several factors may be limiting to plant productivity and nutrient cycling at a given point in time (Burke et al., 1998). Via these mechanisms, fire and grazing may interact at landscape scales to maintain plant-soil C and N pools near some equilibrium level (Seastedt and Knapp, 1993; Blair, 1997; Knapp et al., 1999; Distel et al., 2005). In more arid grasslands, however, water is usually the sole limiting resource, and the influence on nutrient dynamics of changes in the composition of the plant community and (or) in plant tissue chemistry at species level, such as those resulting from fire and grazing, is diminished (Burke et al., 1997, 1998; Hooper and Johnson, 1999; Sembrat et al., 2004).

Grasslands in the Caldenal region of central Argentina have their closest North American analog in the semiarid shortgrass steppe (Burke et al., 1998). However, the climatic signatures of the two regions do not overlap (Paruelo et al., 1995), as reflected vegetationally in the absence of grasses possessing the C<sub>4</sub> photosynthetic pathway from large areas of the Caldenal. Within a single functional group, variation in plant tissue chemistry is limited relative to that between groups (e.g., C<sub>3</sub> versus C<sub>4</sub> grasses) (Wedin and Tilman, 1990; Wedin and Pastor, 1993; Wedin, 1995; Moretto and Distel, 1997; Moretto et al., 2001). The combination of arid climate and reduced functional-group diversity in southern Caldenal grasslands may diminish the influence of vegetation composition on nutrient dynamics (Burke et al., 1998; Wardle et al., 1999). Differences in tissue chemistry among species result in higher decomposition rate of leaves, but small and inconsistent differences in decomposition rate of roots, from low C/N species (Moretto et al., 2001; Moretto and Distel, 2003). Since the root/shoot ratio for these species can be as high as 7:1 (Distel and Fernández, 1986), fire or herbivory-induced shifts in species composition may have limited impacts on plant-soil nutrient dynamics in these Caldenal grasslands.

This study addresses three questions concerning fire and grazing effects on plant-soil nutrient dynamics in grassland ecosystems of the Caldenal. First, do interspecific differences in plant tissue chemistry correspond to differences in soil nutrient content under the canopies of individual plants? Second, do fire and grazing cause intraspecific shifts in plant tissue chemistry? And if so, are these differences in plant tissue chemistry reflected in the makeup and turnover rates of SOM pools? We hypothesize that (1) fire reduces rates of C and N cycling, while grazing increases them, and (2) these changes are due to intraspecific changes in plant tissue chemistry rather than competitive replacements by species with differing tissue chemistry.

## 2. Materials and methods

### 2.1. Study site

The study was conducted on upland grassland sites in the province of La Pampa, Argentina (38°45' S, 63°45' W). Mean annual precipitation is 400 mm, bimodally distributed with peaks in March and October. Mean annual temperature is 15 °C, with mean monthly temperature ranging from a maximum of 24 °C in January to a minimum of 7 °C in July. Soils are classified as Calciustolls, with a petrocalcic horizon occurring at depths of 60 to 80 cm (Cabrera, 1976). The site falls within the Caldén vegetation zone, characterized by clusters of woody plants occurring in an open grassy matrix (Cabrera, 1976; Distel and Boó, 1996). Vegetation is grassland with isolated woody plants. Floristic composition of grasses in the study area is entirely dominated by species possessing the C<sub>3</sub> photosynthetic pathway (Distel and Peláez, 1985).

### 2.2. Interspecific differences in soil C and N

Interspecific differences in soil C and N were evaluated for two grass species. *Stipa tenuissima* is avoided by grazing animals and has higher tissue C/N and lignin/N ratios, while *Poa ligularis* is preferred by grazers and has lower tissue C/N and lignin/N ratios (Distel and Fernández, 1986; Moretto et al., 2001). Soils under the canopies of individual plants of these two species were sampled from two areas with differing management histories, separated by 10 km. In the first area ('natural fire' treatment), domestic livestock has been excluded for 30 years, with natural fires occurring in 1973, 1987, and 1989. In the second area ('prescribed fire' treatment), livestock has been excluded since 1989. Following a period of 30 years with no natural fire, prescribed fires have been implemented in late summer or early fall of 1991, 1994, and 1999. Ten plants of each species were selected for sampling (described below) in each of these areas.

### 2.3. Intraspecific differences in plant and soil C and N

Intraspecific differences in plant and soil C and N were evaluated for *Piptochaetium napostaense*, a preferred shortgrass with lower C/N ratios (Distel and Boó, 1996). Ten individuals of this species were sampled from each of two areas within a live-stock enclosure containing a series of experimental burn

plots. The first of these areas ('fire' treatment) was the experimental prescribed-fire plots described above. The second area ('control' treatment) was a control plot where no fire had occurred for 25–30 years. An additional ten individuals were sampled from a privately-owned and -managed, grazed pasture adjacent to the experimental burn exclosure ('grazing' treatment). This area is managed under a continuous year-long regime at a high stocking rate (6 ha per animal unit, where one animal unit is defined as one mature (455 kg) cow (Society for Range Management, 1974), and was burned in a natural fire in summer 1991. Areas sampled within each treatment were separated from the other treatments by no more than 50 m, in sites with homogeneous environmental characteristics.

#### 2.4. Plant and soil sampling and analysis

Sampling was conducted in October 1999. Aboveground biomass was clipped to the base of the root crown and dried at 60 °C for 5 days. A subsample of dried live biomass from each individual plant was ground to pass through a 250 µm screen in a Wiley mill, and analyzed for C and N concentrations and isotopic composition ( $\delta^{15}\text{N}$ ) on a Carlo-Erba EA-1108 elemental analyzer interfaced with a Delta Plus isotope ratio mass spectrometer (Finnigan MAT, Bremen, Germany).

In all experiments, soil samples were taken from one core per individual plant, 10 cm in diameter to a depth of 20 cm, centered on the root crown. Roots were separated manually, washed in deionized water, and processed and analyzed as described for aboveground biomass. Subsamples of root material were ashed at 600 °C for 4 h to correct for inorganic contaminants (soil particles mainly). All soil samples were stored at 4 °C prior to the analyses described below, except for determinations of inorganic N, which were performed on the same samples immediately upon return from the field, according to the procedure described in Moretto and Distel (2002). Ammonium and nitrate were determined using the steam distillation technique after extraction from soil samples with 2 M KCl (Bremner and Keeney, 1965).

Soil samples were sieved at field moisture content to pass through a 4 mm sieve. Subsamples were removed at this stage for determination of soil microbial biomass carbon (SMB-C) via the chloroform fumigation-incubation method (Voroney and Paul, 1984; Horwath and Paul, 1994; Franzluebbers et al., 1999) and potential C mineralization (Robertson et al., 1999).

Values of SMB-C were calculated without the subtraction of a control, with  $k = 0.43$  (Voroney and Paul, 1984; Horwath and Paul, 1994; Franzluebbers et al., 1999). Potential C mineralization assays were performed on 30 g soil aliquots. The amount of CO<sub>2</sub> trapped in a 1 M NaOH solution was measured at 10, 32, 74, 152, and 208 days (Robertson et al., 1999). The remaining portion of each sample was sieved at field moisture content to pass through a 2 mm sieve and dried at 60 °C for 5 days. A separate subsample of dried soil was ground to pass through a 250 µm screen in a TE250 ring pulverizer (Angstrom, Belleville, MI), and analyzed for concentration of organic C and total N and isotopic composition ( $\delta^{15}\text{N}$ ) of total N on a Carlo-Erba EA-1108 elemental analyzer interfaced with a Delta Plus isotope ratio mass spectrometer (Finnigan MAT, Bremen, Germany). Soils containing CaCO<sub>3</sub> were pretreated with 3 M HCl prior to elemental and isotopic analyses as described in Nieuwenhuize et al. (1994).

Tissue and soil C and N, elemental composition, and SMB-C data were analyzed via an ANOVA model incorporating as factors plant species and fire regime (for *P. ligularis* and *S. tenuissima*) and treatment (for *P. napostaense*). Separate analyses were conducted for shoot, root, and soil data. This portion of the data analysis was carried out in SAS (SAS Institute, Cary, NC, 2002). Potential C mineralization data were used to estimate sizes and mean residence times of 'active' and 'passive' SOC pools via fitting to a four-parameter exponential decay model, of the form  $y = a^e - bx + c^e - dx$ , where  $x$  is the incubation time in days,  $a$  and  $c$  are the size of the active and recalcitrant C pools, respectively, in units of g C kg soil<sup>-1</sup>, and  $b$  and  $d$  are the reciprocals of the mean residence times of the active and recalcitrant C pools, respectively (Collins et al., 2000; Paul et al., 2000). Curve-fitting to the model was carried out in SigmaPlot (SPSS Inc., 1997, Chicago). Statistical differences are reported as significant at  $p < 0.05$ .

### 3. Results

Soils from the prescribed fire treatment in which *P. ligularis* and *S. tenuissima* were sampled had significantly less NO<sub>3</sub><sup>-</sup>-N, NH<sub>4</sub><sup>+</sup>-N, and total N (1.2 vs. 1.5 g kg soil<sup>-1</sup>) than those from the natural fire treatment (Table 1). Soil C/N ratios and  $\delta^{15}\text{N}$  values were higher from the prescribed fire treatment (10.18; 4.49‰) than those from the natural fire treatment (8.25; 3.72‰). For both treatments, soils beneath individuals of *P. ligularis* had higher

**Table 1 – Inorganic N, soil organic carbon (SOC) and total N concentration, C/N ratios, and N isotope ratios, of soils under *Poa ligularis* and *Stipa tenuissima*. Values are means with standard errors in parentheses. Significant differences between species are indicated by letters following values ( $n = 10$ ); between sampling areas, by asterisks following variable names ( $n = 20$ )**

	Natural fire		Prescribed fire	
	<i>P. ligularis</i>	<i>S. tenuissima</i>	<i>P. ligularis</i>	<i>S. tenuissima</i>
SOC (g kg soil <sup>-1</sup> )	12.4 (1.3)	12.8 (1.3)	12.5 (0.6)	12.6 (0.9)
NO <sub>3</sub> <sup>-</sup> -N (µg kg soil <sup>-1</sup> )*	3.4 (0.1)	3.0 (0.2)	1.9 (0.1)	1.9 (0.2)
NH <sub>4</sub> <sup>+</sup> -N (µg kg soil <sup>-1</sup> )*	11.3 (0.5) a	5.9 (0.3) b	8.5 (0.4) a	5.5 (0.3) b
Total N (g kg soil <sup>-1</sup> )*	1.5 (0.1)	1.5 (0.1)	1.2 (0.1)	1.2 (0.1)
C/N*	8.2 (0.5)	8.3 (0.4)	10.2 (0.1)	10.1 (0.2)
$\delta^{15}\text{N}$ (‰)*	3.9 (0.2)	3.6 (0.3)	4.6 (0.1)	4.4 (0.1)

concentrations of ammonium than those beneath individuals of *S. tenuissima*. There were no other significant effects of plant species on soil properties (Table 1).

There were no significant effects of prescribed fire or heavy continuous grazing on C content of shoots or roots of *P. napostaense*. Grazing significantly reduced N content relative to the control in both shoots (8.8 vs. 11.5 g kg dry matter<sup>-1</sup>) and roots (6.7 vs. 9.2 g kg dry matter<sup>-1</sup>). A nonsignificant trend toward higher C/N ratios in both shoots and roots was also evident in response to grazing. Fire significantly increased C/N ratios in shoots (49.87) relative to the control (39.11). Fire also caused nonsignificant trends toward lower N content in shoots and roots and higher C/N ratios in roots. Grazing had no effects on  $\delta^{15}\text{N}$  in roots or shoots, while fire significantly increased  $\delta^{15}\text{N}$  in both shoots (0.74 vs. -0.01‰) and roots (1.30 vs. -0.02‰) relative to the control (Table 2).

Under the canopy of *P. napostaense*, fire and grazing both reduced  $\text{NO}_3^-$  concentrations relative to those in controls, and fire also reduced  $\text{NH}_4^+$  concentration. There were no significant effects of fire or grazing on soil organic C, total N, or C/N ratio of SOM. There were no significant effects of grazing on  $\delta^{15}\text{N}$  of SOM, but fire significantly increased soil  $\delta^{15}\text{N}$  (4.78‰) relative to both the control (4.16‰) and to the grazed treatment (4.02‰). Grazing caused a nonsignificant trend toward higher SMB-C, while fire significantly increased SMB-C (760 vs. 603 mg C kg soil<sup>-1</sup>) relative to the control (Table 3).

There were no apparent effects of grazing or fire on estimated pool sizes and mean residence times of active or recalcitrant SOC pools (Table 4).

## 4. Discussion

### 4.1. Interspecific plant tissue chemistry effects on soil nutrient pools

The lack of species effects on soil organic C and total N pools and fluxes is consistent with previous results on litter decomposition and N mineralization under the canopies of Caldenal grasses. Although the senesced foliage of *P. ligularis* decomposed more rapidly than the senesced foliage of *S. tenuissima*, the roots of both species decomposed at similar rate (Moretto et al., 2001). Moreover, previous results have also failed to demonstrate significant and consistent differences among

species in inorganic N availability and N mineralization rates (Moretto and Distel, 2002; R.J. Andrioli, CERZOS, Bahía Blanca, Argentina, unpublished results). These results suggest that there is a low potential for herbivore- and fire-driven species replacements to cause shifts in soil nutrient cycling regimes in the southern Caldenal grasslands, contrary to what has been documented in mixed C<sub>3</sub>-C<sub>4</sub> systems (Johnson and Matchett, 2001). Within a single functional group (e.g. C<sub>3</sub> grasses), variation in plant tissue chemistry is limited relative to that between groups (e.g. C<sub>3</sub> versus C<sub>4</sub> grasses) (Wedin and Tilman, 1990; Wedin and Pastor, 1993; Wedin, 1995; Moretto et al., 2001; Moretto and Distel, 2003), which may explain the observed results.

### 4.2. Intraspecific effects of fire and grazing on plant tissue chemistry

Grazing caused significant reductions in N content of shoots and roots of *P. napostaense*. The direction of these shifts is contrary to that hypothesized for grazing (Wedin, 1995, 1996). One potential explanation for this finding may be related to plant density relative to and herbivore density. Since *P. napostaense* is preferred by grazers (Bóo et al., 1993), N excreted from ingested foliage may be redistributed to bare soil outside the root radius of the plant, thus breaking the cycle of rapid nutrient cycling via fecal return at the level of the individual plant (Burke et al., 1998). In semiarid grasslands, grazers must cover larger areas than in more mesic systems to generate a given quantity of fecal output. At landscape scales, regrowth in response to herbivory (Busso, 1997), in combination with this relatively high ratio of area grazed to fecal material deposited, may provide a mechanism for reducing tissue N content in preferred grasses. Reduced whole-plant tissue N concentration, coupled with a reallocation of C from roots to shoots in response to defoliation, could explain the lack of significant increase in root C/N ratio. The contrast of these results to reported findings from mesic tallgrass prairie ecosystems (Chaneton et al., 1996; Johnson and Matchett, 2001) may be an effect of climate or of differences in grazing intensity. Long-term, heavy continuous stocking, such as in the grazing treatment in the current study, can have effects on nutrient dynamics similar to those of fire (McNaughton et al., 1988; Seastedt and Knapp, 1993; Van de Vijver et al., 1999).

**Table 2 – C and N concentration, C/N ratios, and N isotope ratios, with standard errors, of shoots (A) and roots (B) of *Piptochaetium napostaense* in fire, grazing, and control treatments. Significant differences between treatments are indicated by letters following values ( $n = 10$ ). Standard errors are in parentheses**

	C (g kg dry matter <sup>-1</sup> )	N (g kg dry matter <sup>-1</sup> )	C/N	$\delta^{15}\text{N}$ (‰)
(A)				
Control	437.8 (7.0)	11.5 (0.6) a	39.1 (2.3) a	-0.01 (0.10) a
Fire	432.1 (9.9)	9.0 (0.6) ab	49.9 (3.3) b	0.74 (0.27) b
Grazing	417.1 (5.7)	8.8 (0.7) b	49.0 (2.8) ab	0.21 (0.17) ab
(B)				
Control	499.4 (23.2)	9.2 (0.7) a	56.8 (4.0)	-0.02 (0.30) a
Fire	435.2 (54.6)	8.7 (0.7) ab	49.3 (6.1)	1.30 (0.40) b
Grazing	432.8 (26.2)	6.7 (0.3) b	66.7 (5.1)	1.14 (0.25) ab

**Table 3 – Carbon and nitrogen concentrations, C/N ratios, C and N isotope ratios, and soil microbial biomass C of soils in the root zone of *Piptochaetium napostaense* in fire, grazing, and control treatments. Values are means ( $n = 10$ ), and standard errors are in parentheses. Significant differences between treatments are indicated by letters following values**

	C (g kg soil <sup>-1</sup> )	NO <sub>3</sub> <sup>-</sup> -N (μg kg soil <sup>-1</sup> )	NH <sub>4</sub> <sup>+</sup> -N (μg kg soil <sup>-1</sup> )	N (g kg soil <sup>-1</sup> )	C/N	δ <sup>15</sup> N (‰)	SMB-C (mg C kg soil <sup>-1</sup> )
Control	12.1 (1.0)	7.3 (0.3) a	7.1 (0.3) a	1.0 (0.1)	12.0 (0.3)	4.2 (0.2) a	603 (49) a
Fire	12.0 (0.6)	3.0 (0.2) b	3.8 (0.3) b	1.0 (0.1)	11.5 (0.3)	4.8 (0.1) b	760 (30) b
Grazing	11.8 (1.7)	3.3 (0.4) b	8.0 (0.3) a	1.1 (0.1)	10.9 (0.2)	4.0 (0.2) a	672 (55) ab

The significant increase in shoot C/N ratio of the fire treatment agrees with predictions and is similar to results from annually-burned plots in tallgrass prairie ecosystems (Johnson and Matchett, 2001). Significant increases in δ<sup>15</sup>N values of shoots and roots in response to fire suggest that volatilization losses of aboveground biomass N during combustion may result in a more ‘open’ N cycle [one in which the proportion of N lost from the system is greater than that retained in plants and soil (Austin and Vitousek, 1998; Handley et al., 1999)]. The lighter <sup>14</sup>N isotope is more readily volatilized, leading to <sup>15</sup>N enrichment (larger δ<sup>15</sup>N values) of the residual N]. Cook (2001) reported the opposite trend from sites in Australia, with more frequent fire leading to less positive δ<sup>15</sup>N values. However, that author notes that interpretation of stable N isotope signals may be complicated by simultaneous gradients of fire frequency and precipitation. Other factors also influence foliar δ<sup>15</sup>N values, but the similar response of both soil and plant δ<sup>15</sup>N values in the study supports our interpretation of these as fire treatment effects.

Both the direction and degree of fire and grazing effects on vegetation depend on the environmental context, and the result of alterations in one factor is dependent upon the other (Hobbs, 1996). The ultimate outcome may be determined by differences between the two pathways of biomass removal (fire vs. herbivory) in the total amount of N lost from the system. Future quantification of these losses may help to elucidate the reasons for varied responses to fire and herbivory in different grassland ecosystems (Coughenour, 1991; de Mazancourt et al., 1998, 1999; Hamilton et al., 1998; de Mazancourt and Loreau, 2000).

#### 4.3. Intraspecific plant tissue chemistry effects on soil nutrient pools

Although spatial separation of sampling areas precludes straightforward interpretation of the differences, soils beneath both *P. ligularis* and *S. tenuissima* in areas of prescribed fire had lower inorganic and total N and higher C/N ratios than those in areas under a natural fire regime. This finding,

in contrast to many published reports of fire effects on soil inorganic N (Wan et al., 2001), suggests that stoichiometric plasticity within individual species might provide an alternate mechanism of linkage between fire-induced changes in vegetation composition and alterations in soil nutrient dynamics. Whether via species replacement or species-independent reductions in tissue N, reduced N availability and quality of SOM in more frequently or recently burned areas are consistent with some results from other grasslands (Blair, 1997; Sanchez and Lazzari, 1999; Johnson and Matchett, 2001; Fynn et al., 2003).

Both fire and grazing reduced NO<sub>3</sub><sup>-</sup>-N under the canopy of *P. napostaense*, while fire alone reduced NH<sub>4</sub><sup>+</sup>-N. Sanchez and Lazzari (1999) observed a different pattern of inorganic N response to fire, but the difference may be related to the time of sampling. A significant increase in δ<sup>15</sup>N values of SOM in burned treatments again suggests that the mechanism of N loss in fire treatments may be volatilization from aboveground plant tissue and litter (Hobbs et al., 1991). However, the lack of significant differences in C/N ratio of SOM between fire and control treatments does not reflect such a loss. Moreover, soil total N under the canopy of *P. napostaense* varied little between treatments. Thus, it appears that the effects of prescribed fire are concentrated on the smaller pool of available N, with changes in the total soil pool manifested over longer time periods, if at all (Wan et al., 2001). A similar pattern was observed in the different responses of labile versus total soil C pools. Greater SMB-C in the fire treatment may be due to increased root productivity caused by reduced N availability, increased inputs of decomposable C via greater turnover of fine roots, or the stimulation of microbial growth by increased soil temperatures following burning (Seastedt and Knapp, 1993; Hamilton and Frank, 2001; Johnson and Matchett, 2001; Hubbard, 2003). The slightly greater estimated active SOC pool in the fire treatment is consistent with this result, and suggests that effects of changes in plant tissue chemistry influence soil nutrient dynamics primarily via the small labile fraction of SOM (Wedin and Pastor, 1993; Wedin, 1995, 1996). The influence of root dynamics on C and N cycling in

**Table 4 – Estimated pool sizes and mean residence times (MRTs) of SOC in soils from control, burned, and grazed treatments in the rooting zone of *Piptochaetium napostaense* ( $n = 10$ )**

Treatment	Active pool		Recalcitrant pool	
	MRT (days)	Size (g C kg soil <sup>-1</sup> )	MRT (years)	Size (g C kg soil <sup>-1</sup> )
Control	6.7	0.6	13.9	12.4
Burned	6.9	0.7	13.9	12.4
Grazed	6.4	0.6	13.9	13.8

this ecosystem is probably great (Semmartin et al., 2004), with root/shoot biomass ratios for grasses of the region as high as 7:1 (Distel and Fernández, 1986; Moretto and Distel, 1997; Moretto et al., 2001). Both a uniform 1:1 ratio of above:below-ground NPP (Epstein et al., 2002) and a stable depth distribution of roots and SOM (Gill et al., 1999) have been reported across a precipitation gradient spanning the entire North American Great Plains. However, there is substantial regional and local spatial variation in these values and in their response to fire and herbivory (Lavado et al., 1996; Derner et al., 1997, 2006; Kelly and Burke, 1997; Turner et al., 1997; Frank and Groffman, 1998; Augustine and Frank, 2001; Flynn et al., 2003).

One aspect of grazing impact on soil nutrient cycling not addressed in this study is that in overgrazed Caldenal grasslands, perennial grasses are often replaced as dominants by exotic annual forbs (e.g. *Medicago minima*, *Erodium cicutarium*; Distel, personal observation). Such a shift, particularly to leguminous N-fixers such as *M. minima*, could have profound consequences for C and N cycles (Chaneton et al., 1996; Knops et al., 2002). Likewise, a more comprehensive understanding of ecosystem C and N dynamics in Caldenal grasslands requires an assessment of material flows between the herbaceous matrix and those elements of the landscape with higher abundances of woody plants. Soils under woody vegetation in the Caldenal display different patterns of N response to burning (Sanchez and Lazzari, 1999). It is not clear to what degree the grassland 'patches' in *Prosopis* savannas function as independent nutrient-cycling elements in the landscape. Within those patches, our results suggest that fire and grazing are unlikely to have significant impacts on the sequestration of atmospheric C in soils and vegetation. However, continued heavy grazing and/or the absence of fire can increase the abundance of woody shrubs, converting herbaceous landscape elements to a shrubland physiognomy (Distel and Boó, 1996; Boó et al., 1996). Such shifts in vegetation can have marked consequences for ecosystem C and N dynamics (Asner et al., 1997; Holland et al., 1999; Schimel et al., 2000; Reich et al., 2001; Jackson et al., 2002).

## 5. Conclusions

This study presents evidence that intraspecific shifts in plant tissue chemistry constitute a mechanism of fire and grazing effects on plant-soil C and N cycles in Caldenal grasslands. These shifts appear to be manifested via alterations in dynamics of N rather than C. Negative feedbacks between plant tissue chemistry and soil nutrient dynamics (Tateno and Chapin, 1997; Ritchie et al., 1998; Knops et al., 2002) may be a more appropriate model for this system than positive feedbacks (Wedin, 1995; Wedin and Tilman, 1996). There were no apparent shifts in quality, size, or turnover time of recalcitrant or total SOC pools in response to fire or grazing. This may be due in part to the lack of C<sub>4</sub> species in southern Caldenal grasslands, which limits the potential of shifts in species composition to alter ecosystem C dynamics (Wardle et al., 1999). The role of water as the primary limiting factor on productivity and N mineralization in these semiarid grasslands

may be more important (Burke et al., 1997, 1998; Hooper and Johnson, 1999; Semmartin et al., 2004).

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