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## Original article

## Fire and grazing differentially affect aerial biomass and species composition in Andean grasslands

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## ABSTRACT

Grazing and fire have been the most common disturbances in many grasslands ecosystems for many centuries. However, some mountain regions are currently experiencing a decrease in land use, and therefore in frequency or intensity of these disturbances. In this study, we evaluated how fire and grazing affect vegetation structure in mountain grasslands of NW Argentina. We hypothesized that they would have differential effects on plant species richness, vegetation composition and aerial biomass dynamics, predicting that fire would have a stronger effect on these variables than grazing. We tested this hypothesis by performing a controlled field experiment in which we manipulated fire and compared grazed plots with ungrazed exclosures, simulating current (high frequent fires and low livestock load) and future (fire suppression and grazing exclosure) scenarios. We recorded total of 90 species with 40 shared among all treatments. Tussock grasses (*Elionurus muticus*), followed by three shrubs represented the main contribution to live biomass in all treatments. Species richness, equitativity and diversity were higher in burned plots. Multivariate ordination indicated that burning is more important than grazing in determining plot to plot similarity in species composition. Burning reduced total aerial biomass, standing dead biomass and litter, as well as live biomass, that was also reduced by grazing. Burning also reduced standing dead biomass and litter proportions, but increased live biomass contribution, showing a more evident effect within the grazed plots. Burning, seasonality and growing season had significant effects on the relative contribution of all biomass categories. Biomass consumption showed a strong seasonality, being significantly higher in January of both growing seasons, and it was not affected by burning. We conclude that under the current fire and grazing scenario, fire plays a more important role than grazing in shaping these grasslands dynamics.

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## 1. Introduction

Grazing and fire are the most common disturbances in many grassland ecosystems around the world and they play a key role in shaping grassland structure and dynamics (McNaughton et al., 1993; De Baro et al., 1998; Oesterheld et al., 1999; Geist and Lambin, 2002; Bond, 2005). Together with climate, they are the main factors involved in grasslands development and maintenance (Oesterheld et al., 1999).

Livestock raising represents one of the major causes of tropical forest deforestation (Geist and Lambin, 2002) and is one of the

most important land uses in montane grasslands and forest ecotones (Eckholm, 1975). Grazing has been found to selectively affect grassland structure, increasing spatio – temporal heterogeneity, decreasing species dominance, and promoting forbs and unpalatable vegetation (Collins, 1990; Collins and Smith, 2006). This increase in diversity is often associated to the colonization by exotic species (Sala et al., 1986; Chaneton and Facelli, 1991; D'Antonio and Vitousek, 1992; Milchunas and Lauenroth, 1993).

Importantly, in mountain grasslands many management practices associated to grazing involve intentional burning during the dry season (Scott, 1977; Schmidt and Verweij, 1992; Hofstede et al., 1995; Grau and Brown, 2000). Fire has shown to promote resprouting and to encourage the development of more palatable life forms, however, in some cases, it can increase non palatable shrubs density and remarkably alter grassland structure (Liedloff et al., 2001). Fire is controlled by ignition sources (Flannigan and Wotton, 1991; Pyne, 1993) and by biomass fuel availability, which

Abbreviations: B–G, burned–grazed; B–UG, burned–ungrazed; UB–G, unburned–grazed; UB–UG, “control”: unburned–ungrazed.

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in turn is affected by livestock biomass removal (Scott, 1977; Savage and Swetnam, 1990; Cochrane and Laurance, 2002) and by climate that regulates fuel production and desiccation (Swetnam, 1993; Kitzberger et al., 1997; Grau and Veblen, 2000).

In Andean montane ecosystems grasslands cover extensive areas, and they include both natural grasslands and those that have an anthropogenic origin (Ellenberg, 1979; Sarmiento and Frolich, 2002; Aragón et al., 2006; Carilla and Grau, 2010). Certain climatic and topographic conditions (e.g. abrupt forest – grassland ecotones, coexistence of both ecosystems at the same elevation and slope, no differences in geological formation or soil humidity with the surrounded forest) can be used as an indication of human influence. Importantly, grasslands are often associated to a long and intense land use history, which led to the degradation of their soils (Lægård, 1992; Cavelier et al., 1998). However, in the last 50 years subtropical mountains of NW Argentina as other Andean landscapes, had experienced a decrease in grazing intensity associated to human migration from rural to semi-urban and urban areas (Preston et al., 1997; Aide and Grau, 2004; Grau and Aide, 2007). Contrary to expectations, fire regime did not show the same trend. Anthropogenic fires became a cultural behaviour, independent of livestock load (Carilla and Grau, 2010). Interestingly, there is an active politics of fire suppression implemented mainly by the protected areas managers. These opposite trends are expected to produce changes in disturbance regimes that can, in turn, affect plant communities in different ways.

Fire and grazing can have similar as well as differential effects on grassland composition and structure. On the one side, they are both defoliating agents (Bond and Keeley, 2005), and therefore they reduce standing biomass, which modifies environmental variables (e.g. light and water availability), and plant productivity (Pucheta et al., 1998; Hubbard, 2003). Both disturbances may affect species richness in a similar way and force the selection for similar general traits, such as reduced plant height (Noy-Meir and Kaplan, 2002), serotony/thorns (Bond and Van Wilgen, 1996; Young et al., 2003), promotion of C4 species (Collins et al., 1998; Spajosevic et al., 2010) and exotic plants (Sala et al., 1986; D'Antonio and Vitousek, 1992). On the other side, fire and grazing can have differential effects on vegetation since fire acts as a not selective grazer (Bond and Keeley, 2005). The effect of grazing is usually differential among different biomass compartments, life forms or species (Díaz et al., 1994, 2001; Collins et al., 1998; Pucheta et al., 1998).

The effect of fire and grazing simultaneously has been scarcely assessed despite of their importance for shaping grassland structure, and affecting functioning and plant productivity (Fuhlendorf and Engle, 2004). The combined effect of fire and grazing depends on diverse factors such as previous history of grazing, plant productivity, and environmental moisture, which together influence the fire regime (Milchunas and Lauenroth, 1993; Valone and Kelt, 1999). Controlled field studies are needed to isolate fire and grazing effects and make specific predictions about their interaction in particular systems. Manipulative experiments become particularly useful to answer this kind of questions. Few studies have examined the effect of fire and grazing simultaneously and in an experimental set up (e.g. Noy-Meir, 1995; Valone and Kelt, 1999), and this approach so far was not used to explore the role of these disturbances in subtropical montane grasslands. Studying fire and grazing in combination reflects more accurately how they interact in most grasslands, and contributes to the overall understanding of this ecosystem functioning.

The aim of this study was to analyze how fire and grazing affect vegetation structure in mountain grasslands of NW Argentina, specifically using two possible scenarios of current levels and future trends. We hypothesized that fire and grazing interaction affect plant species richness, vegetation composition and aerial

biomass dynamics differentially, than if they act separately, mainly because the fire effect may be damped by grazing consumption of fuel biomass. More specifically, we expect that fire, as a non selective herbivore (Bond and Keeley, 2005), may reduce aerial biomass in a larger degree than grazing, but in a more generalized manner, while the effect of grazing would be limited to certain biomass categories or life forms. We tested these hypotheses by performing a controlled field experiment in which we manipulated fire in extreme situations (i.e., high frequent fires as in present times and fire suppression as in future trends), and compared grazed plots with low livestock load (current situation) and ungrazed enclosures fenced at the beginning of the experiment (extreme future trends).

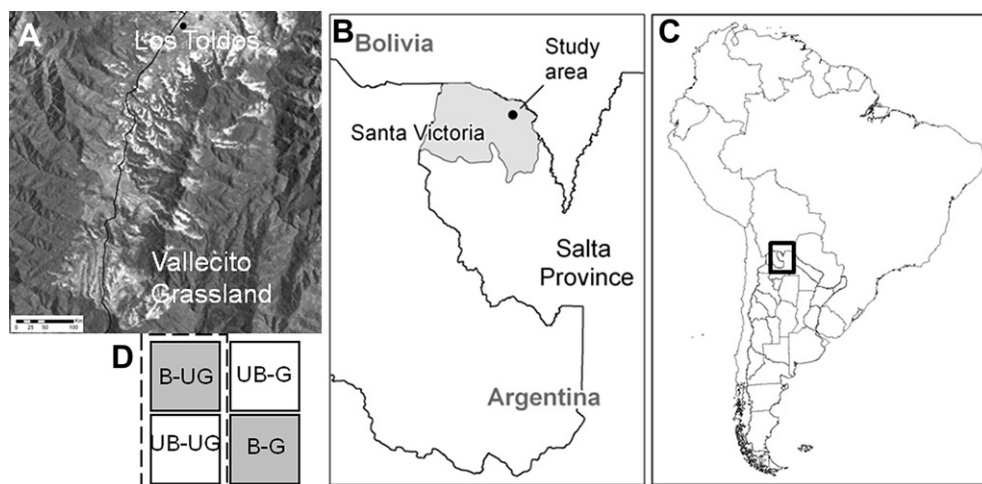
## 2. Materials and methods

### 2.1. Study area

This study was carried out in the valley of Los Toldos (22° 30' S, 64° 50' W), department of Santa Victoria, Salta, Argentina, located at 1600 m.a.s.l. (Fig. 1). This altitudinal level is classified as *Upper Mountain forest* within the phytogeographic province of the Argentinean Yungas (Cabrera, 1976). The study area is a mosaic of mountain grasslands, shrublands and secondary forest patches dominated by *Alnus acuminata* and *Podocarpus parlatorei*, encompassing an area of approximately 6000 ha. The mean annual temperature is 11.7 °C (Easdale et al., 2007), with an average precipitation of approximately 1300 mm (average value from 1972 to 1989) that is concentrated during summer months (November–March) (Bianchi and Yañez, 1992). As meteorological data from Los Toldos is relatively short (1972–1989), we used other meteorological stations close to the study area, such as Aguas Blancas (22° 43' S 64° 22' N, 405 msnm, 80 km South from Los Toldos; Red Hidrológica Nacional, 2006) to compare rainfall temporal patterns, especially during the two years of the experiment.

Extensive cattle raising, with no fences limiting individual properties is the most common land use. Signs of soil erosion are frequent elements in the landscape may be as the result of the combination of grazing, frequent burning, high rainfall and steep slopes (Easdale et al., 2007). Data for the whole department, together with information provided by locals, suggest that grazing load at Los Toldos is currently low (0.3–0.4 livestock ha<sup>-1</sup>), c. 35% less than at the beginning of the century (Gil Montero, 2005). The pastoral system involves transhumance, a seasonal movement of cattle between altitudinal sites. Cattle are driven up to highland grasslands like the valley of Los Toldos at the beginning of the warm period (October), and they are brought back to mid-altitude and piedmont forests in March (Grau and Brown, 2000). With these movements they avoid the period of shortage of forage in highland grasslands (April–August approximately). Summer grazing is usually preceded by spring intentional burnings. The extension and frequency of burning depends on the proximity of settlements, on weather conditions when fire starts (i.e., wind, temperature, soil humidity), and on fuel biomass availability (Carilla and Grau, 2010). Fire events, spread throughout the landscape, occur every year, but a given spot is seldom burned two years in a row (Carilla and Grau, 2010). As a result of this management practice, the landscape in this area is currently a mosaic of vegetation patches differing in the time since the last burning.

Soils are predominantly clayey and silty franc varying from haplic phaeozems (young and dark soils, rich in organic matter) to eutric regosols (Nadir and Chafatinos, 1990). We did preliminary measurements of soil surface temperature and humidity in the study area, and they showed a strong seasonality, but apparently no difference between areas that were or not burned. Soil surface



**Fig. 1.** Study area. (A) Satellite image of the valley of Los Toldos, Department of Santa Victoria, Province of Salta. Los Toldos village is located in the northern valley and Vallecito, where the experiment was established, in the South. (B) Location in NW Argentina and (C) in Argentina. (D) Experimental design: grey squares represent burned plots and white squares, unburned ones (here in one of the possible random combinations). Dash line represents the wire fence (ungrazed treatment). Treatment codes: B–G (burned–grazed), B–UG (burned–ungrazed), UB–G (unburned–grazed), UB–UG (unburned–ungrazed).

temperature was maximum in October (21.4 °C) and January (20.5 °C), and lowest in March (15.9 °C) and August (14.5 °C). This seasonality was a little more evident in burned plots. Soil humidity varied from 30.8% (in areas that were grazed and unburned) to 60.3% (in sites that were ungrazed and unburned), but there was not a clear difference between burned and non burned areas.

## 2.2. Experimental design

The experiment was established in August 2001 in Vallecito, ca. 7 km South from Los Toldos village, an area of extended grasslands (Fig. 1A). We used a factorial design with two factors (Grazing and Burning), and two levels (treatment and no treatment) of each factor, for a total of four treatment combinations: burned–grazed (B–G), burned–ungrazed (B–UG), unburned–grazed (UB–G), and unburned–ungrazed (UB–UG, “control”; Fig. 1D). The four treatments were established in five 40 × 40 m blocks (i.e., replicates) spread around the valley, under similar conditions of slope (<1%), forest distance, soil and parent rock. Treatment levels were chosen representing extreme current and future conditions. Half of each block (20 × 40 m) was fenced and therefore excluded from grazing, mimicking extreme future situation of no livestock. Grazed plots were not manipulated, maintaining the current low livestock load. The burning treatment was then randomly assigned within each half; consequently, each treatment was established in 20 × 20 m plots. A buffer zone of 1 m was left between plots. Plots assigned to burned treatments were burned in August 2001, 2002 and 2003 mimicking the burning season of this area in an extreme current scenario of annual frequency fires. Unfortunately, parts of three of the plots in the unburned treatment were accidentally burned in spring 2003, but the remaining plots received no fire during the three years of the experiment. In addition, we established two 1 × 1 × 1 m mobile cages in each grazed plot ( $N = 20$ ) to estimate livestock biomass consumption. We estimated plant productivity in grazed (using the mobile cages) and ungrazed plots following Pucheta et al. (1998).

## 2.3. Sampling and data analysis

We collected aerial biomass in three 0.5 × 0.5 m subplots placed randomly in each 20 × 20 m plot, four times per year between October 2001 and August 2003 for a total of eight sampling periods:

January (summer), March (autumn), August (winter) and October (spring). Vegetation sampling in August was performed before burning. Biomass was classified into three categories: live biomass, standing dead, and litter. Live biomass was further classified into seven different life forms: erects, prostrate (stolonifers) and rosettes dicots, ferns, graminoids (graminoids of small size, Poaceae, Juncaceae and Cyperaceae family), tussock grasses (typical tufted grown grasses of the Poaceae family) and woody species (as in Pucheta et al., 1998). All vegetal material was separated, dried to constant weight at 70 °C, and weighted. We estimated biomass consumption as the difference in live biomass collected inside and outside the cages (within the grazed plots) at each sampling date (every two–four months). Cages were removed after each vegetation harvest and moved to a different spot within the same plot to avoid any potential effect of the manual removal of biomass (Oesterheld and McNaughton, 2000). We recorded the position of the cages to avoid using the same spot at any other sampling date.

Species composition and abundance was assessed on January 2004 (after three burning periods) by estimating species aerial cover through the Van der Maarel scale (Van der Maarel, 1979), in four 2 × 2 m subplots randomly established within each plot ( $N = 16$ ). Van der Maarel scale was used to maximize less abundant or rare species. Cover categories were transformed to percentage cover for the analyses. We also computed species diversity through the Shannon–Weaver index and Equitativity (O'Neill et al., 1988).

To measure compositional similarity among plots we calculated Sorensen Index, and then used a Non-metric multidimensional scaling (NMDS) to reduce the dimensionality of the similarity matrix (Kruskall, 1964). This ordination technique is one of the most effective methods for community data since it is robust and independent from assumptions about the distribution of species along the gradients underlying the ordination (Kenkel and Orlóci, 1986; Minchin, 1987; McCune and Grace, 2002). Data matrix was based on species cover per plot, calculated averaging 4 m<sup>2</sup> subplots (four subplots per treatment in each block), and we only considered species recorded in more than one plot. We used the starting coordinates based on a solution obtained with Autopilot mode in PC-Ord 5.0 (McCune and Mefford, 1999) with the slow and thorough option (number of real runs = 40 and maximum number of iterations = 400). NMDS axes were rotated to align the direction of greatest variation with the horizontal axis (Varimax rotation option). Percent of variation in the original data that was explained



by the ordination was calculated through Pearson  $r^2$ , correlating the distance between the plot scores in the ordination space and the distance in the original matrix (McCune and Grace, 2002). We used a three-dimensional configuration because the final stress was lower than 20, which indicate a relatively good agreement between graph configuration and the similarity matrix (Legendre and Legendre, 1998), and it was significantly different from chance (Montecarlo: 250 runs with randomized matrix,  $p = 0.004$ ). We computed Kendall-tau correlations between plot scores and species cover per plot to identify species that were driving the ordination. ANOVA and correlations were performed with STATISTICA 6.1 (StatSoft, 2003). For botanical nomenclature we followed Zuloaga and Morrone (1999a,b).

We used a repeated measures ANOVA to test for differences in the amount and proportion of dry biomass in the different categories and life forms, using seasonal variation (four sampling dates per growing season) as a repeated factor, and growing season (two levels), and burning and grazing (and their interaction) as fixed factors. In this way we could explore seasonal trends, and potential changes in the effect of burning and grazing between the first and the second growing seasons. We defined a growing season as the period between October of one year and August of the next. In addition, we analyzed the treatments effects on species richness, diversity and equitativity using a two-way ANOVA. Data were log-transformed when normality assumptions were not met.

### 3. Results

#### 3.1. Species composition and richness

A total of 90 species were recorded in the experiment, with 40 species shared among all treatments and 24 recorded in only one treatment, but with very low cover (0.82%). We identified 27 erects, 18 prostrates, 13 graminoids, 7 rosettes, 5 tussock grasses, 3 ferns and 10 woody species. The most abundant life form corresponded to tussock grasses (45.2% of the total cover recorded in the 4 m<sup>2</sup> subplots), followed by woody species (27%), while rosettes were the least represented (5.7%). Species richness (R), diversity (H') and equitativity (J) were significantly higher in burned plots (R: 41.3, H': 2.8 and J: 0.8) than in unburned ones (R: 35, H': 2.3 and J: 0.6) ( $F_{(1,11)} = 5.90$ ,  $p = 0.03$ ;  $F_{(1,11)} = 18.35$ ,  $p < 0.01$ ; and  $F_{(1,11)} = 11.96$ ,  $p < 0.01$  for R, H' and J respectively), while grazing did not show any significant effect on these variables.

The most abundant species in all treatments was the tussock grass *Elionurus muticus*; with an average of 44% of total cover (ranging from 28.4% in B–G to 69.2% in UB–UG), while the next 10 most abundant species represented an average of 39.4% of total cover. Three woody species followed in abundance: *Baccharis coridifolia* (from 4.6% in UB–G to 12.3% in B–UG), *Eupatorium* sp. (4% in UB–G and UB–UG and 9.8% B–UG), and *Baccharis rufescens* (from 2% in UB–G and UG to 7.7% in B–UG). *Pteridium arachnoideum* was the most abundant fern (with highest cover in B–UG, 7.5%) and *Cuphea* sp. the most common prostrate (with it highest cover in UB–G, 5.6%). Twenty-five species were present only in burned plots, while seven species, mostly erects were recorded exclusively in unburned ones. Fourteen species were present only in grazed plots, and 12 were only recorded in ungrazed ones. In all cases the exclusive species represent a small percentage of the total cover (less than 4%).

Plot ordination in the NMDS space separated burned plots from unburned ones (in the positive side of axis I and negative side of axis II), while there was no evident ordination of grazed–ungrazed plots (Fig. 2). Hence, burning is more important than grazing in determining plot to plot similarity based on species composition. *Agrostis* sp., *Sisyrinchium* sp. and *Eringium* aff. *agavifolium* were the species most negatively correlated with this axis (associated with

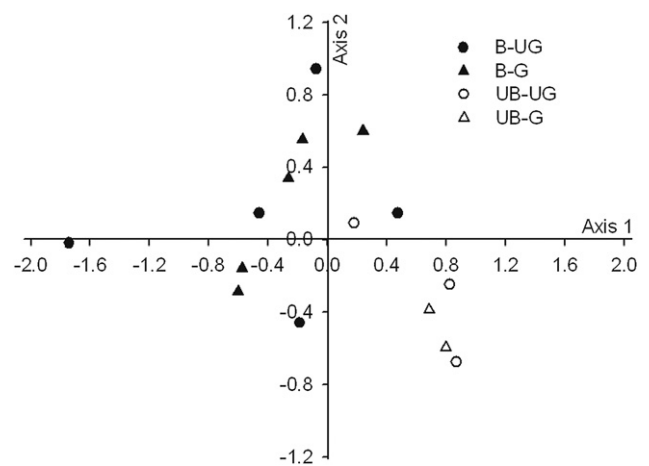


Fig. 2. Ordination of plots in a multivariate space defined by Non-Metric Multidimensional Scaling (Stress of the three-dimensional solution = 4.02, Montecarlo test,  $p = 0.004$ ; Variance explained computed as Pearson  $r^2 = 0.95$ ). For treatment codes see Fig. 1.

burned plots), while *E. muticus* showed a positive correlation (associated with unburned plots).

#### 3.2. Changes in the aerial biomass of the different biomass categories and life forms and in their relative contribution

Total aerial biomass as well as standing dead, litter and live biomass were differentially affected by burning and grazing. Total aerial biomass was significantly higher in unburned plots than in burned ones at all sampling dates ( $F_{(1,32)}$  for Burning = 151.38,  $p < 0.01$ ), and the same pattern was true for standing dead and litter (Fig. 3) ( $F_{(1,32)}$  for Burning = 120.25 and 115.98 respectively,  $p < 0.01$ ). The seasonality of total biomass showed similar annual trends in all treatments with maxima in August of both growing seasons. Mean total biomass was approximately twofold higher in unburned plots (603.7 g m<sup>-2</sup> mean values considering UB–G and UB–UG) than in burned ones (318 g m<sup>-2</sup>, mean values considering B–G and B–UG) in almost all months. Standing dead and litter were

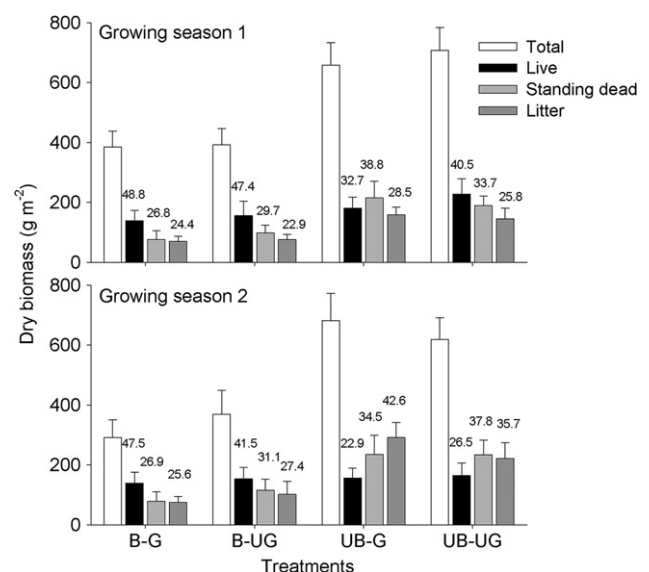


Fig. 3. Total, standing dead, litter and live biomass (g m<sup>-2</sup>) variation (mean and standard error) in the different treatments for the two growing season. Number above bars indicates biomass percentage (%). For treatments codes see Fig. 1.

not significantly affected by grazing, while they all showed seasonal variability (i.e., both biomass categories peaked in August) and a tendency to increase in the second growing season ( $F_{(1,96)}$  for Seasonality = 55.34 and 44.11,  $p < 0.01$ ;  $F_{(1,32)}$  for Growing season = 3.4,  $p = 0.07$ ; and  $F = 27.32$ ,  $p < 0.01$  respectively). Importantly, live biomass showed a rather different pattern. It was significantly reduced not only by burning but also by grazing ( $F_{(1,32)}$  for Burning = 17.65;  $F_{(1,32)}$  for Grazing = 6.49,  $p < 0.01$ ), and showed a distinct seasonality (i.e., with a peak in January or March coincident with the rainy season;  $F_{(1,96)}$  for Seasonality = 89.84,  $p < 0.01$ ) and a decrease in the second growing season ( $F_{(1,32)}$  for Growing season = 7.19,  $p = 0.01$ ; Fig. 4A). In the first growing season live biomass of unburned plots was on average, 27% higher than biomass of burned plots, but this difference was mainly due to the unburned–ungrazed plots. This difference decreased to less than 10% in the second growing season.

The relative contribution of the different biomass categories showed similar trends to the ones described considering the absolute amount. Burning, seasonality and growing season had significant effects on the relative contribution of all biomass categories. Burning significantly reduced standing dead and litter proportions and increased live biomass contribution ( $F_{(1,32)}$  for Burning = 53.06, 17.21 and 174.02 respectively,  $p < 0.01$ ). Live biomass proportion also showed a significant burning  $\times$  grazing interaction ( $F_{(1,32)}$  for Burning  $\times$  Grazing = 6.03,  $p < 0.01$ ) since the effect of burning was more evident within the grazed plots (Fig. 4B). During most of the year, live biomass proportion was approximately 16% higher in burned plots than in unburned ones, and among them it was even lower in the grazed plots. Importantly, the difference in live biomass between burned and unburned plots was more evident during January and March. Live biomass contribution was maximum in January ( $F_{(1,96)}$  for Seasonality = 6.92,  $p < 0.01$ ), while standing dead and litter peaked in August ( $F_{(1,96)}$  for Seasonality = 62.72, and 51.87 respectively,  $p < 0.01$ ).

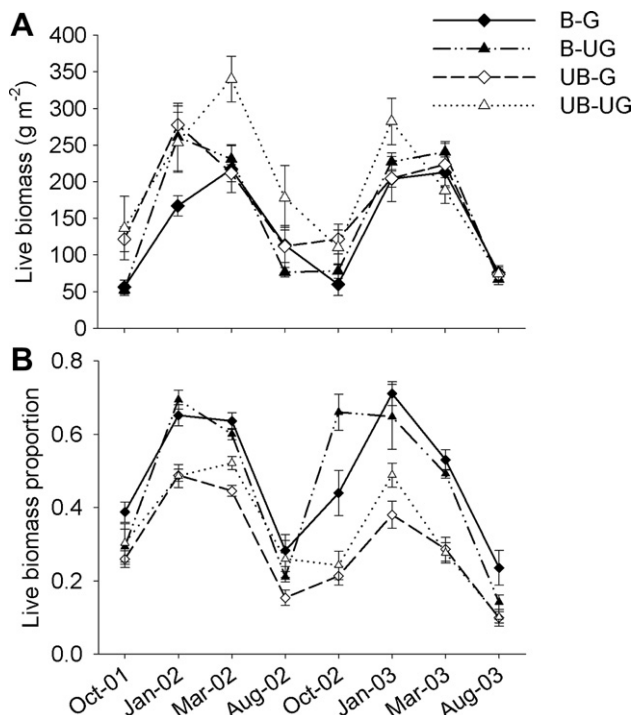


Fig. 4. Seasonal variation of live biomass a) gross values and b) relative contribution comparing different treatments (mean and standard error). For treatments codes see Fig. 1.

Woody species ( $78.5 \text{ g m}^{-2}$ , averaging all sampling dates in all treatments) and tussock grasses ( $64.2 \text{ g m}^{-2}$ ) represented the main contribution to live biomass in all treatments, while rosettes represent the less abundant life form. Biomass of tussock, graminoids, erects and prostates were significantly affected by burning, but in different ways. Tussocks were more abundant in unburned plots, while graminoids, erects and prostates showed the opposite trend (Table 1). Neither burning nor grazing had a significant main effect on the biomass of woody species, but there was a burning  $\times$  grazing interaction ( $F_{(1,32)}$  for Grazing  $\times$  Burning = 4.86,  $p < 0.05$ ). Woody species decreased with burning in ungrazed plots, but showed almost no change in grazed plots. All life forms showed seasonal variation with maximum values in January or March. Growing season was only important in the biomass of woody species, that significantly decreased in the second growing season ( $F_{(1,32)}$  for Growing season = 21.78,  $p < 0.01$ ).

The proportions of the different life forms were differentially affected by burning, seasonality and growing season (Table 1). Woody species proportion was highest in burned plots, while tussock contribution prevailed in unburned ones. The effect of burning in the proportion of erects and prostates changed with seasonality (i.e., there was a burning  $\times$  seasonality interaction), with differences between burned and unburned only in October (erects) or October and March (prostate). During these dates the proportions of these two life forms were significantly higher in burned plots. Growing season was only important for woody species and tussock grasses proportions. Woody species reduced their contribution in the second year, while tussock increased it. Grazing did not significantly affect the proportion of any of the life forms. Importantly, we have to keep in mind that when using proportions, a change in the relative contribution of a given life form does not necessary mean a change in its absolute biomass amount (see Table 1 for the absolute values).

### 3.3. Biomass consumption and productivity

Biomass consumption, calculated as the difference between live biomass inside and outside the cages located in grazed plots, showed seasonal variation with its maximum during January of both years (repeated measures ANOVA:  $F_{(6,48)}$  for Seasonality = 2.40;  $p = 0.04$ ). Consumption in this month was more than twofold that of any of the remaining sampling dates (Fig. 5). Although seasonal variation in consumption was more evident in burned plots, consumption was not significantly affected by burning (repeated measures ANOVA:  $F_{(1,8)}$  for Burning = 0.26;  $p = 0.6$ ). Mean consumption was  $51.4 \text{ g m}^{-2}$  and  $72.5 \text{ g m}^{-2}$  in unburned and burned plots respectively, which corresponded to a 4.7% and 10.5% of the total biomass, respectively (averaged overall sampling dates). As expected, standing dead and litter were not consumed by cattle (i.e., no differences inside and outside the cages), and they only showed differences in response to fire.

Aerial net primary productivity (ANPP) was highly seasonal and it was concentrated during the summer months (between October and March; Table 2). Unfortunately, we did not sample enough data points to perform a statistical analysis, but it seems that there was a tendency to an increase in ANPP in grazed plots. Burning, on the other hand, did not seem to have an effect.

## 4. Discussion

In this study, we found that fire and grazing affect biomass distribution and diversity in different ways. On the one hand, the effect of burning was highly evident promoting richness, diversity and equitativity, and also affecting species composition and aerial biomass. On the other hand, the effect of grazing at the current low

**Table 1**  
Biomass life form ( $\text{g m}^{-2}$ ) and their percentage in parenthesis, during each growing season. Treatment codes: B–G (burned–grazed), B–UG (burned–ungrazed), UB–G (unburned–grazed), UB–UG (unburned–ungrazed).

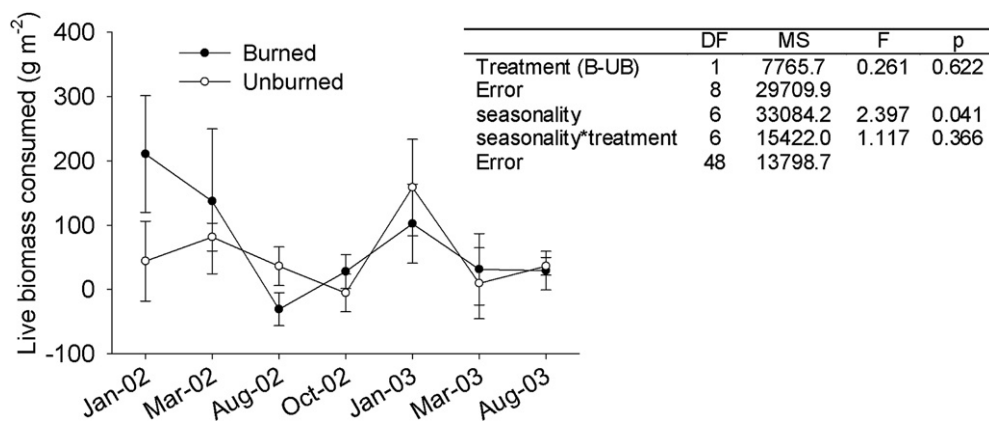
Life forms	Growing season 1				Growing season 2			
	B–G	B–UG	UB–G	UB–UG	B–G	B–UG	UB–G	UB–UG
Woody	92.42 (51.1)	78.50 (56.6)	125.85 (55.4)	77.11 (49.7)	46.49 (29.7)	71.69 (54)	66.14 (40.3)	46.49 (45.1)
Tussock	68.13 (37.7)	41.49 (29.9)	84.58 (37.2)	50.98 (32.6)	90.98 (58.2)	38.66 (29.1)	81.68 (49.8)	90.98 (37)
Graminoid	2.33 (1.3)	5.18 (3.7)	3.26 (1.4)	5.42 (3.5)	3.08 (2)	7.11 (5.4)	2.60 (1.6)	3.08 (2.9)
Erect	1.38 (0.8)	1.66 (1.2)	1.19 (0.5)	2.14 (1.4)	0.69 (0.4)	1.14 (0.9)	0.87 (0.5)	0.69 (1.2)
Prostrate	8.92 (4.9)	7.48 (5.4)	8.83 (3.9)	13.76 (8.9)	7.27 (4.7)	6.55 (4.9)	9.49 (5.8)	7.27 (9.9)
Fern	7.15 (4)	3.71 (2.7)	3.04 (1.3)	4.34 (2.8)	7.23 (4.6)	4.38 (3.3)	2.92 (1.8)	7.23 (2.3)
Rossete	0.41 (0.2)	0.56 (0.4)	0.53 (0.2)	1.49 (1)	0.54 (0.3)	3.24 (2.4)	0.38 (0.2)	0.54 (1.5)
Total	180.73	138.58	227.27	155.24	156.28	132.78	164.07	156.28

livestock load was only detectable in live biomass (both absolute amount and proportion). Plant diversity promoted by burning was found in other studies (Vogl, 1974; Harrison et al., 2001), and when grazing was simultaneously considered, it had in general, a less marked effect (Valone and Kelt, 1999), similar to our results. As expected, burning decreased total biomass, as well as in the individual biomass categories (live, standing dead and litter), and also standing dead and litter proportions. Consequently, burning enhanced live biomass proportion according to the traditional belief that fire stimulates vegetation resprouting. The same pattern was also found if we consider dead/live ratio (data not shown). Burning was associated with a significant decrease in this ratio, especially in grazed plots. Total biomass increases in the second growing season, was probably associated to a moister year; rainfall in 2003 was 1614 mm compared to historical mean of 1213 mm during 1945–2006 period (data from Aguas Blancas). Importantly, even though we found what we expected considering the relative importance of both disturbances (i.e., fire, that was applied with an extreme frequency, was the main driver), the effect of fire was not as general as we predicted, affecting particular life forms in different ways. Grazing did not have an effect on any of the life forms (proportions or absolute amounts), or species composition, not in agreement to what we previously hypothesized.

Biomass values in Los Toldos resemble that of other mountain or mesic grasslands, but differences appear if we consider burned and grazed treatments. Biomass in burned and ungrazed plots showed a more similar pattern when compared with other mesic grasslands, than biomass in the unburned and grazed ones. When taking into account grazed/ungrazed treatments, we found that total biomass in ungrazed plots ( $590.1 \text{ g m}^{-2}$ ) was higher than reported by Pucheta et al. (1998) ( $404 \text{ g m}^{-2}$  in two years of exclusion) for

montane grasslands of Pampa de Achala, Córdoba, with drier conditions (800 mm precipitation and 2000 m.a.s.l., approximately). Biomass from grazed plots in our experiment was more than two times higher ( $617.3 \text{ g m}^{-2}$ ) than biomass of grazed areas reported by these authors ( $269.7 \text{ g m}^{-2}$ ), probably reflecting the current low livestock load in our study area. Comparing burned/unburned treatments, Briggs and Knapp (1995) found, in the central US tallgrass prairie, similar total biomass values for annually burned upland sites ( $362 \text{ g m}^{-2}$ ) and higher for annually burned lowland sites ( $506.1 \text{ g m}^{-2}$ ) than in our study ( $348.1 \text{ g m}^{-2}$ ). However they found lower biomass values in both unburned lowland and upland sites ( $404.1$  and  $357.1 \text{ g m}^{-2}$  respectively) than in our experimental unburned plots ( $590.1 \text{ g m}^{-2}$ ). These results suggest that fire, the most important disturbance in several grasslands, could lead ecosystems to share similar structural characteristics (i.e., converging towards similar biomass values).

Quantifying grazing effects on these grasslands at current stocking level resulted more difficult than quantifying fire effect. Since cattle are widespread in the valley, their effect on soil and vegetation (nutrients return and tissue removal) is heterogeneously distributed across the landscape (Semmartin and Oesterheld, 2001). The differential effect of fire and grazing on vegetation observed in this study may be related to a combination of several factors, such as fire frequency (Collins and Smith, 2006; Spajosevic et al., 2010), the history of grazing (Milchunas et al., 1990, 1998), the current livestock load, and the spatial and time-scale of the experiment (Pucheta et al., 1998). Historical records of cattle stock (Reborati, 1996) and information provided by National livestock censuses for the department of Santa Victoria, indicated a high livestock load during at least 250 years, followed by a decrease in domestic animals density during the second half of



**Fig. 5.** Live biomass consumed in burned and unburned cages (mean and standard error). Table indicates F values of the repeated measurement ANOVA.

**Table 2**Net primary productivity (NPP) ( $\text{g m}^{-2} \text{d}^{-1}$ ). For treatment codes see Table 1.

	B–G	B–UG	UB–G	UB–UG
Jan-02	4.94	3.20	3.07	1.80
Mar-02	3.12	0.00	0.76	1.44
Aug-02	0.00	0.00	0.00	0.00
Oct-02	0.23	0.03	0.50	0.00
Jan-03	3.79	2.30	3.71	2.64
Mar-03	0.78	0.15	0.79	0.00
Aug-03	0.00	0.00	0.00	0.00

the 20th century (Carilla and Grau, 2010; Grau et al., 2010). Even though historical records are not available for our study area, grazing at Los Toldos seems to have followed the same general trend. Although information about pre-colonization grazing load is lacking, one may suppose that some cervids were present in this area (e.g. *Hippocamelus antisensis* and *Mazama americana*) (Regidor, 2000; Merino, 2006), and that the domestication of Andean camelids by natives, recorded for the Bolivian Andes, could have reached this area as well (Wing, 1986). The abundance of *E. muticus*, typical of grazed sites (Killen, 1991) in all treatments, could suggest a relative long history of grazing in Amerindian times and higher grazing intensity in the past. Concepts of resilience and alternative stable state may be useful for explaining the low effect of grazing exclusion on vegetation (Wilson and Agnew, 1992; Sunding et al., 2004). Grasslands with a long history of grazing are more resilient to temporal and spatial variation of grazing intensity (Cingolani et al., 2005), showing a range of structural and compositional reversible situations, maintaining a relatively constant high diversity. In some cases, the transition along this range, could lead grassland community to an alternative stable composition barely associated to livestock stocks variations (Cingolani et al., 2008). Due to the relatively long history of grazing in these grasslands, livestock introduction in 15th century, probably did not cause a remarkable shift in vegetation composition. In addition, a two-year grazing exclusion by fencing is perhaps not long enough to observe differences in vegetation responses.

As stated above, burning had significant effects on aerial biomass (both total amounts and relative contribution), richness, diversity and species composition. However, the relative magnitude of the effects on these variables differs. Burning reduced total biomass by approximately 50%, while the changes in species richness between burned and unburned plots represented a difference of less than 15%. The increase in biomass in unburned plots was mainly accounted for one life form, tussock grasses, and a single species *E. muticus*. In other words, a large change in a structural attribute (i.e., biomass) was not translated to a compositional change. This is also reflected in the fact that, although many unique species grow within burned plots, they represent a very small portion of these plots biomass. Overall, grazing had a null or minor effect on biomass distribution and species composition, as other studies found (Diaz et al., 2007), but when it had an effect, the patterns found were, in general, coincident with previous works. Different life form proportions were not considerably affected by grazing, except prostrate species that tended to increase in grazed plots (higher in the second year of the experiment). The increase in species of this growth form is a common response associated to herbivore resistance (Pucheta et al., 1998; Nai-Bregaglio et al., 2002; de la Orden et al., 2006). No changes in abundance of palatable plants (mainly graminoids) were associated to grazing, similar to what Diaz et al. (2007) found, and opposite to the results reported by McNaughton (1993), meaning that the trends are still not clear.

Even though the response of the different biomass categories in our study was similar to the pattern mentioned in previous works,

our results contradicted what several studies have documented about the relative contribution of woody species and tussock grasses. Previous works found that woody species increased and tussock grasses decreased with fire suppression (Collins, 1992; Aragón et al., 2006), while we found the opposite. Interestingly, the pattern found in Los Toldos was similar to the one described by Briggs et al. (2002) where grazing modified the fire effect, increasing woody species density. Fire frequency applied in this experiment, one annual fire, vs. more than 4–5 year fire frequency in Collins (1992) and Aragón et al. (2006), and the lack of information about the previous fire events in the experimental site, may explain the described trend. Fire intensity is related to fuel biomass availability (Bachelet et al., 2000; Liedloff et al., 2001), which is contributed mainly by tussock grasses (Burkart, 1969). Annual fire frequency and grazing reduced tussock grasses biomass, consequently fire may not be intense enough to eliminate woody species. In addition, fire releasing resources and reducing grasses competition, may cause the observed effect on woody species (Schultz et al., 1955).

Our results suggest that fire plays a more important role than grazing in maintaining montane grasslands in Los Toldos, like in many grasslands and savannas worldwide (Bond, 2005). However, we acknowledge that we evaluated the role of these two different disturbances under extreme scenarios in our study area, representing current and the most probable future trends: burning frequency was at the uppermost extreme (i.e., once a year), while grazing was at a low intensity (i.e., less than 0.3 animals  $\text{ha}^{-1}$ ). The relative importance of grazing may change if grazing intensity increases, although given the regional trend, this is highly unlikely to occur in the future. It is important to highlight that burning is still a very common practice in the valley, even under the current low livestock load. In addition, other studies in this area have pointed out that forest tree recruitment (*A. acuminata*) is concentrated approximately 5 years after each fire event (Grau and Veblen, 2000; Grau, 2004). In Vallecito grasslands we did record an increase in woody species biomass, but no forest tree recruitment, even though, distance to propagule source is relatively close (less than 2 km), and the typical pioneer tree, *A. acuminata* is wind dispersed. Importantly the enhancement in tree establishment following fire events is supposed to be related to competition release caused by the elimination of grasses. However, it is associated to more sporadic fires (e.g. 20 years approximately) that would allow survival of forest tree saplings (Grau and Veblen, 2000). As we mentioned earlier we have several reasons to assume that these grasslands have an anthropogenic origin, and they would persist in this state, resistant to forest tree establishment, as a consequence of recurrent fires (e.g. less than 10 years fire frequency; Carilla and Grau, 2010). Hence, even under the current low grazing intensity, fire is important enough to warranty these grasslands persistence, either by causing tree sapling mortality or modifying environmental variables such as soil nutrient availability (Collins, 1992). It is important to highlight that these anthropogenic grasslands show a relatively high species richness (Aragón et al., 2006), and that they significantly increase gamma diversity of the region. This may be an important issue to take into account when designing conservation strategies for this area.

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