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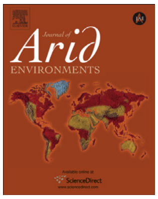

Continuous moderate grazing management promotes biomass production in Patagonian arid rangelands

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Domestic grazing effects on primary productivity and community structure are controversial in rangeland ecology and frequently misunderstood. Although directly related with secondary production, biomass stock and biomass production at species level (biomass composition) has been relegated in field studies, especially in arid rangelands co-dominated by woody species. We estimated grazing effects on aboveground biomass in a temperate mixed grass-shrub steppe of Patagonia. We compared exclusion of sheep with two levels of continuous grazing: moderate (light) and intensive sheep grazing in an average precipitation year. Total green biomass (productivity) was twice as high in moderately grazed paddocks as in those without grazing and intensively grazed pastures, while standing dead grass biomass stock only decreased in intensive grazing. Shrub biomass was not modified by grazing management. In addition, grazing modified grass specific biomass composition, thus diminishing biomass quality in intensively grazed areas. This work provides evidence that in arid rangelands, continuous moderate grazing management could be an effective tool to increase productivity compared to grazing exclusion. Furthermore, moderate grazing would not cause major undesired changes in species composition. However, a potential risk of land use intensification exists because intensive grazing could decrease biomass production as well as promote negative composition changes.

1. Introduction

Grazing by domestic livestock is the most common and widespread land use in arid rangelands (Milchunas and Lauenroth, 1993; Oesterheld et al., 1999; Asner et al., 2004) and is identified as one of the major causes of desertification (Brown et al., 1997). However, estimating its impacts on primary production and community structure has been a controversial topic in rangeland ecology (Belsky, 1992; Milchunas and Lauenroth, 1993; Oesterheld et al., 1999; Briske et al., 2008; Wu et al., 2013). In general, maintaining domestic grazing through time (i.e. years) under confined areas (fenced) reduces the forage value of rangelands due to depletion of some preferred species and their replacement by non-preferred species (e.g. James et al., 1999; Tobler et al., 2003), along with productivity and vegetation cover decline and soil erosion increase (Milchunas and Lauenroth, 1993; Brown et al., 1997). Nonetheless, in some rangelands, wild or domestic herbivores can promote productivity and preferred species compared to ungrazed situations, creating grazing lawns of high forage quality (Cargill and Jefferies, 1984; McNaughton, 1984; Posse et al., 2000; Cingolani et al., 2005). In arid grasslands, neutral, positive and negative plant species responses to grazing have been recorded, although species richness has not shown significant changes (Fensham et al., 2010, 2014). Grazing intensity could be an important mechanism which determines the impact of herbivores on vegetation responses (Oesterheld and Semmartin, 2011). Hence, evaluating different grazing intensities can help to refine grazing management practices in order to promote biomass production without undesired changes in species composition (Cingolani et al., 2005; Oesterheld and Semmartin, 2011). In particular, woody-grass steppes are challenging because grazing can trigger different and opposite woody-grass ratio responses (Sankaran et al., 2005), from shrub encroachment to shrub decrease (Cipriotti and Aguiar, 2012). In this paper, we estimated biomass production of grass and shrub species in a temperate grass-shrub steppe under different historical grazing intensities.

Coexistence of herbaceous and woody species has relevant ecological implications for ecosystem function, and there has been

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an increasing interest in understanding grass-woody balance (see for a recent review Sala and Maestre, 2014). Primary productivity variation of herbaceous and woody components is one of the major conundrums in rangeland ecology (House et al., 2003). Grazing can differentially affect grass and woody species through direct and indirect effects (Cipriotti and Aguiar, 2005, 2012). Because of rapid grass—woodland transitions, identifying productivity controls of both life forms is especially important in mixed communities (Sala and Maestre, 2014).

Globally, there is more information about grazing effects on community species composition than about grazing effects on net primary productivity and plant biomass (Milchunas and Lauenroth, 1993). Even less information is available on grazing effects of biomass production at species level. In arid mixed rangelands, this is probably the result of the difficulty of estimating biomass of woody co-dominant species (House et al., 2003). Furthermore, the management of much of world's grazing systems is primarily based upon changes in species composition. In general, species composition is estimated along with richness and species abundance. The latter is evaluated through frequency or cover in order to estimate diversity. However we think that, despite the difficulty and the expense of estimation (Byrne et al., 2011), biomass production of dominant species is the key attribute of vegetation that should be managed. The use of plant cover to estimate abundance has generated controversy since plant structure could generate differences in biomass that are not captured with cover, especially in ecosystems co-dominated by grass and woody species (Montès, 2009; Oñatibia et al., 2010). In this sense, grazing management should be based on biomass composition, which is what herbivores select and consume.

Our objective was to study sheep grazing effects on aboveground biomass in a mixed grass and shrub steppe of Patagonia. We estimated biomass (total, green and standing dead) and density of dominant grass and shrub species in the peak of production during early summer. Our assumption was that green biomass in peak production may be considered a good proxy of aboveground annual productivity in these sites, which present a brief and pronounced growing season as was proposed by Sala and Austin (2000). Our general hypothesis was that continuous and intensive domestic grazing history reduces total biomass production due to intense and sustained defoliation. By grazing history, we refer to more than a decade of grazing; under this time span plant demographic dynamics develop and community changes occur. Due to sheep selectivity, we expect a higher effect on preferred species and, along time, a biomass and density decrease. However, if grazing intensity is moderate, this reduction caused by defoliation could be compensated through two different mechanisms. On the one hand, grazing can promote an optimization process, increasing the productivity of defoliated species (McNaughton, 1979) and, on the other hand, depending on less preferred species response (higher abundance or not), total biomass production may increase or be maintained. Because of this possible positive effect of grazing on plant biomass, we propose that domestic herbivore exclusion will not necessarily raise biomass production.

2. Materials and methods

2.1. Study site description

We worked in a grass-shrub steppe area of 300 km^2 located in South Central Patagonia, Chubut province, Argentina, including the Rio Mayo INTA Experimental Station and privately owned neighboring rangelands (lat 45º24′ S, long 70º15′ W). This steppe is mostly used for wool production and has been grazed by sheep for more than one hundred years. Grazing management is extensive, in large paddocks (frequently around 1000 to 5000 ha), continuously grazed (Golluscio et al., 1998). Mean monthly temperature is between 2 °C in July and 14 °C in January. Average annual precipitation is 154 ± 44 mm, and most rainfall occurs between May and September. Few dominant perennial grasses and shrubs contribute approximately 96% of total biomass (Fernández et al., 1991), and mean aboveground net primary production is 560 kg ha^{-2} yr^{-1}, half of which corresponds to grasses and half to shrubs (Jobbágy and Sala, 2000). The dominant grass species are *Pappostipa speciosa* Trin. et Rupr., *Pappostipa humilis* Cav., *Poa ligularis* Nees ap. Steud and *Bromus pictus* Hook. The dominant shrub species are *Mulinum spinosum* Cav. Pers, *Adesmia volckmannii* Philippi and *Senecio filaginoides* De Candolle. Sheep and native herbivores are very selective and select their diet from these dominant grass and shrub species.

2.2. Grazing treatments

We worked in a group of paddocks distributed over a 150 km^2 homogenous plateau. We studied three grazing management treatments: ungrazed (exclosure > 20 years), moderately grazed and intensively grazed fields. Grazing management has not experienced changes during the last decade. During dry years, only moderate grazed paddocks experienced planned reduction in sheep numbers. Each management treatment was represented by three different paddocks or fields (replicates), except the exclosure treatment for harvesting grass biomass. The moderately grazed treatment correspond to paddocks (around 1000 to 1200 ha) where stocking rate has been around 0.2 sheep ha^{-1} yr^{-1} for more than two decades. This grazing pressure could also be defined as continuous (year round) light grazing. The intensively grazed pastures were paddocks (around 1200 to 1500 ha) where the stocking rate over the last 20 years was about 0.4 sheep ha^{-1} yr^{-1} year round (Cipriotti and Aguiar, 2005). In grazed pastures, we avoided areas near watering points or fencing to prevent grazing sampling in areas of local high grazing pressure. To evaluate the non-grazing treatment, we only had one exclosure (8 ha in area) to utilize for destructive sampling. This exclosure was established in 1983. The three replicates of grass biomass were inter-dispersed in this area. We are aware of the implications from inferences based on pseudo replication (Hurlbert, 1984). Therefore, we added two other exclosures, installed in 1954 and 1972, to perform non destructive sampling (shrubs density and biomass, and grass density). In this way we complied with exclusion's management guidelines in the Experimental Field and increased robustness of our inferences. Exclosures installed in 1954 and 1972 were 2 and 5 ha in size, respectively. Because the 1983 exclosure was large, we assumed that grass biomass samples represented a large proportion of the potential variation of excluded plant communities. Additionally, we have measured that exclosures of different ages (three exclosures of this study and two additional exclosures installed in 1994 and 1998) do not differ in several variables associated to grass aboveground biomass (grass total and specific density, individual plant size, population structure of all dominant grass species and grass total and specific cover (Oñatibia, 2013)). Furthermore, all study sites correspond to the same plant community. Therefore, we assumed that differences in composition and aboveground biomass among treatments can be attributed to grazing effects (Cipriotti and Aguiar, 2005). The grass harvest and shrub study was performed in January, at the end of the growing season (peak of green biomass). Annual water year precipitation of the previous year that included this growing season was 156 mm, similar to an average year.

2.3. Biomass estimation

We sampled aboveground grass biomass in five plots of 1 m^2

(5 m × 0.2 m) per pasture under the three grazing conditions ($n = 3$). In each pasture, we selected representative areas of the community near the center of the paddock. To control local grazing condition we visually estimated species composition, fecal pellet density, morphology of preferred species, soil surface condition or erosion signs, and sheep footprint density. Inside these areas, we randomly located the five 5 m × 0.2 m plots. In each plot, we estimated specific density by counting all individuals, harvested all aboveground biomass of dominant perennial grasses and classified them by species (*P. speciosa, P. humilis, P. ligularis, B. pictus,* and other species). We also collected soil cover litter which proved impossible to identify to the species level. In the laboratory, we separated three specific biomass categories: green, senescent (yellow) and standing dead. Green and senescent were considered live biomass. All material was oven-dried (65 °C for 72 h) and weighed.

We estimated aboveground shrub biomass along the grazing gradient ($n = 3$) in 2 plots of 50 m^2 (50 m × 1 m) per pasture through a non destructive method (Oñatibia et al., 2010). In each pasture, we selected representative areas of the community near the center of the paddock and inside these areas we randomly located the two 50 m × 1 m plots. In each plot, we evaluated all established shrubs of the three dominant species (*A. volckmannii*, *M. spinosum* and *S. filaginoides*). We measured species density conducting a census within the plot and we measured height and two diameters of the crown (the longest and the one perpendicular to it) of each individual. Likewise, we additionally estimated the proportion of dead crown. These variables allowed us to estimate live and standing dead biomass (g $plant^{-1}$) using specific allometric equations adjusted to the study area (Oñatibia et al., 2010).

From biomass data we estimated primary productivity of both life forms under the three grazing managements ($n = 3$). We assumed that green biomass at the end of the growing season (as estimated in this study) is equivalent to one year growth (productivity). This approach was supported by previous studies (e.g. Jobbágy and Sala, 2000). Additionally, this method reduces estimation errors in relation with multi-sampling approaches that consider several time intervals (Sala et al., 1988; Sala and Austin, 2000). In shrub species, we applied specific coefficients (Oñatibia et al., 2010) to total live biomass in order to exclusively estimate the productivity of green twigs, leaves and flowers, discarding woody live tissue produced in previous years. We also estimated average biomass consumption by sheep in moderately and intensively grazed conditions by multiplying the sheep stocking rate by the estimated consumption per sheep per year (365 kg of dry matter; Agricultural Research Council, 1980). Due to the simplicity of estimation and the limitations of this approach (we estimated only average), in the graph we presented average sheep consumption as a visual comparison.

2.4. Data analysis

We used analysis of variance (ANOVA) to evaluate the effect of grazing on total, live and standing dead aboveground biomass of each life form (grasses and shrubs) comparing each category of biomass among grazing levels. We conducted a two-way ANOVA between grazing level and species for grasses and shrubs, and we also analyzed the effect of grazing on biomass of each species using ANOVA. To evaluate the effect of grazing on the proportion of dead biomass of grasses and shrubs, we conducted a two-way ANOVA between species and grazing level for each life form. Within the grass analysis, we removed *B. pictus* because it presented very low values of biomass under grazed conditions. Specific density and total density of each life form were compared among grazing levels using one way ANOVA. Bonferroni correction for specific one way ANOVA was applied within each life form. Finally, the effect of grazing on aboveground primary productivity was analyzed using one way ANOVA among grazing intensities for each life form.

Analyses were performed using Infostat software (2008). We controlled data normality and variance homogeneity through Levene's test using absolute residuals. We used Tukey test for mean comparisons post-hoc ANOVA. Values in the text and graphs are mean ± standard error. Results were presented separating grass and shrub categories because of the different estimation approaches.

3. Results

Total aboveground biomass stock (live and standing dead) of grasses was on average 46% higher in moderately grazed and ungrazed areas (5154.9 ± 354.4 and 4349.7 ± 105.2 kg ha^{-1}, respectively) than in intensively grazed sites (2561.2 ± 245.6 kg ha^{-1}) ($P < 0.05$). Green and senescent (live) biomass was higher ($P < 0.05$) in moderately grazed sites (1432.6 ± 171.9 kg ha^{-1}) than in those ungrazed (728.1 ± 38.5 kg ha^{-1}) and intensively grazed (807.7 ± 94.5 kg ha^{-1}), while standing dead biomass showed the same pattern as total biomass (Fig. 1). Grazing historical intensity did not affect shrub total aboveground biomass ($P = 0.40$, mean overall grazing conditions 4677 ± 236 kg ha^{-1}). Live and standing dead biomass of shrubs did not differ among grazing intensities (Fig. 1). Values of shrub live biomass were highly variable under intensively grazed conditions. Litter biomass was close to 600 kg ha^{-1} under ungrazed and moderately grazed conditions (610.78 ± 35.8 and 557.3 ± 33 kg ha^{-1}, respectively), which was greater ($P < 0.05$) than litter biomass from intensively grazed areas (266 ± 28.5 kg ha^{-1}).

Aboveground biomass of grass species responded differently to grazing history (Fig. 2a). *P. ligularis* total biomass exceeded 2000 kg ha^{-1} in ungrazed sites, while it decreased by half in moderately grazed paddocks, presenting the lowest biomass in those intensively grazed ($P < 0.05$). *B. pictus* decreased its biomass under both grazed conditions in relation to exclosure ($P < 0.05$), although it did not dominate under this latter condition (Fig. 2a). *P. speciosa* had higher biomass in moderately grazed plots (values close to 3000 kg ha^{-1}) than in ungrazed and intensively grazed plots ($P < 0.05$). *P. humilis* was highly variable and showed a tendency to increase its biomass under intensively grazed conditions ($P = 0.15$) compared to ungrazed and moderately grazed paddocks

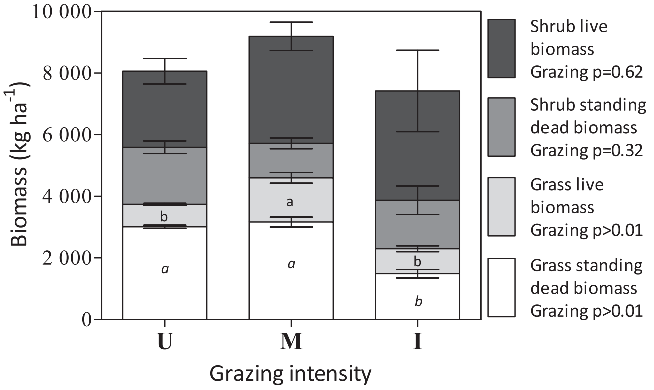

Fig. 1. Total aboveground live and standing dead biomass of grasses and shrubs under three grazing intensities (U: Ungrazed; M: Moderately grazed; I: Intensively grazed). Bars correspond to mean values and vertical lines indicate standard errors. Different letters indicate significant differences ($P < 0.05$) among grazing intensities within each biomass category and life form (Tukey test).

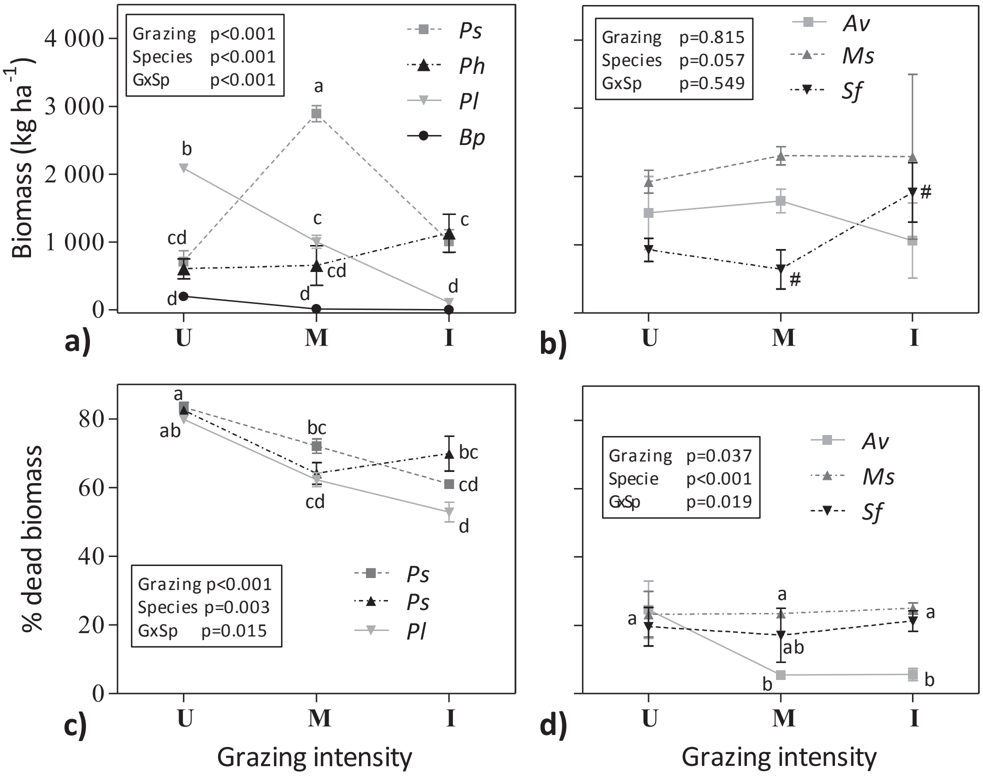

Fig. 2. Aboveground biomass stock under three grazing levels (U: Ungrazed; M: Moderately grazed; I: Intensively grazed) of dominant **a)** grass species (*Pl*: *Poa ligularis*, *Bp*: *Bromus pictus*, *Ps*: *Pappostipa speciosa* and *Ph*: *Pappostipa humilis*), **b)** shrub species (*Av*: *Adesmia volckmannii*, *Ms*: *Mulinum spinosum* and *Sf*: *Senecio filaginoides*) and Percentage of standing dead biomass under three grazing levels of **c)** grass species and **d)** shrub species. Symbols correspond to mean values and vertical lines indicate standard errors. Tables indicate *P*-values resulting from two-way ANOVA between species and grazing levels. Different letters indicate significant differences ($P < 0.05$) resulting from a two way ANOVA between grazing intensity and species (Tukey test). Numerals (#) indicate marginal differences for individual species ANOVA ($P = 0.10$) which were not found in the two-way ANOVA.

(Fig. 2a). Biomass of other grass species was reduced; *Carex* sp. values were 46 kg ha^{-1} on average and did not differ among grazing levels ($P = 0.7$) and *Hordeum* sp. presented significant amounts of biomass only in ungrazed sites (82 kg ha^{-1} on average) and no biomass of this species was found under grazed conditions. However, it was highly variable and there were no significant differences among grazing levels ($P = 0.34$).

Plant density of *P. ligularis* and *B. pictus* decreased from the exclosures to the grazed conditions, mainly in intensively grazed areas (Table 1). However, *P. ligularis* differences were not statistically significant after applying Bonferroni corrections. *P. speciosa* increased its density under grazing conditions presenting marginal differences and *P. humilis* showed a tendency to increase in intensively grazed sites (Table 1).

From the three shrub species studied, only *S. filaginoides* showed a marginally significant increase in biomass ($P = 0.10$) and density ($P < 0.05$) under intensive grazing (Fig. 2b, Table 1). Additionally, *M. spinosum* exhibited great variability in intensively grazed fields (Fig. 2b).

The percentage of total standing dead biomass of grasses was higher ($P < 0.05$) under ungrazed conditions (>80%) than under moderate and intensive grazing (<73%). Dead biomass of *P. ligularis* and *P. speciosa* gradually decreased with grazing intensity, while *P. humilis* only exhibited differences between ungrazed and moderately grazed sites, being values higher under the first condition (Fig. 2c). The proportion of dead crown of *M. spinosum* and *S. filaginoides* shrubs (standing dead biomass) was similar and was not affected by grazing (22% on average). On the contrary, *A. volckmannii* showed lower percentage of dead crown in grazed plots than in ungrazed sites, where it did not differ from *M. spinosum* and *S. filaginoides* (Fig. 2d).

Grass annual aboveground average productivity was twice as

Table 1
Specific density (individuals·m^{-2}) of dominant grass and shrub species in three grazing levels (U: Ungrazed; M: Moderately grazed; I: Intensively grazed). The table values indicate the mean ± standard deviation. Different letters indicate significant differences ($P < 0.05$, without Bonferroni correction) for each species among grazing intensities (Tukey tests). Values of significantly affected species are in bold. Significant *P*-values after 5% Bonferroni corrections were lesser than 0.0125 for grass species and lesser than 0.0167 for shrub species.

Life form	Species	Grazing intensity			
		P-value	U	M	I
Grasses	*Poa ligularis*	0.036	**7.17 ± 0.25 a**	**7.28 ± 1.12 a**	**3.22 ± 1.16 b**
	Bromus pictus	0.002	**1.45 ± 0.15 a**	**0.72 ± 0.15 b**	**0.28 ± 0.05 b**
	Pappostipa speciosa	0.076	4.28 ± 0.05 a	7.89 ± 0.95 a	7.45 ± 1.40 a
	Pappostipa humilis	0.188	2.78 ± 0.29 a	2.50 ± 0.73 a	4.17 ± 0.67 a
Shrubs	*Adesmia volckmannii*	0.368	0.14 ± 0.06 a	0.17 ± 0.02 a	0.09 ± 0.02 a
	Mulinum spinosum	0.561	0.31 ± 0.06 a	0.29 ± 0.07 a	0.22 ± 0.06 a
	Senecio filaginoides	0.012	**0.31 ± 0.02 a**	**0. 09 ± 0.03 b**	**0.39 ± 0.08 a**

high ($P < 0.05$) in moderately grazed sites than in those ungrazed and intensively grazed sites. No difference was observed when comparing ungrazed and intensively grazed sites (Fig. 3). Similarly to other variables, total shrub productivity did not differ among grazing intensities (Fig. 3).

4. Discussion

Our results showed that continuous moderate grazing promotes a grass biomass increase, without major undesired changes in species composition or the grass-shrub ratio. On the contrary, both domestic grazing elimination and grazing intensification reduce biomass production. These patterns would not drastically change by adding the forage consumed by sheep. Considering this consumption, productivity was approximately 40% reduced in ungrazed sites and 20% in intensively grazed sites, compared with those moderately grazed. These results provide evidence backing the hypothesis of grazing optimization process in this temperate mixed steppe. Only two variables were measured associated to ecosystems condition (biomass production and composition). However, the higher aboveground biomass in moderately grazed areas is in line with higher forage provision (Oñatibia et al., 2015) and, compared to ungrazed areas, no changes were observed in soil organic carbon (Golluscio et al., 2009) and species richness (Perelman et al., 1997). Thus, this work support the idea that management of natural vegetation through domestic grazing with moderate stocking rate would be the best alternative of land use in this Patagonian grass-shrub steppe.

The recommended stocking rate of moderately grazed areas in the study site was estimated using the Pastoral Value of each paddock. This criterion can be extrapolated to other rangelands, thus achieving a similar grazing pressure to the one in the moderate grazing treatment of this work. The method is based on the relative frequency of all species composing the community, weighed by their specific quality index, which depends on the sheep preference (see Golluscio et al., 1998 [appendix] and Elissalde et al., 2002 for methodological details). As a result of this management strategy, the proportion of aboveground primary production consumed by sheep under moderately grazed conditions is less than 10%. This consumption is close to that found in ecosystems grazed by native herbivores and it is lower than the average consumption by domestic herbivores in ecosystems with similar annual productivity (Golluscio et al., 1998; Oesterheld et al., 1999).

Grass aboveground biomass stock and grass production were maximized under moderately grazed conditions. Grazing exclusion did not change total biomass of grasses in relation to moderate grazing, although this was primarily due to accumulation of dead material. Live biomass and biomass production decreased in the exclosure of this study compared to moderate grazed pastures, as found in other rangeland ecosystems (Oesterheld et al., 1999). This would be the result of moderate grazing, which can promote an optimization process of production by compensatory growth of plants (McNaughton, 1979), together with an acceleration of nutrient cycling by physical disturbance and by feces and urine excretion. Furthermore, we found that a community level process, such as variation in species biomass and density driven by sheep grazing, also explains this increment through overcompensation. Contrarily, under intensively grazed conditions, the values of total grass aboveground biomass decreased by almost half compared to moderately grazed paddocks. Recovering this reduction in biomass could take more than a decade, given the low productivity of this system (Jobbágy and Sala, 2000). These results indicate that the objective of achieving a greater secondary productivity per area unit by intensifying grazing reduces the natural capital, and sheep production would not be sustainable. The reason for this is that intensive domestic grazing drastically reduces the amount of preferred species biomass and density, compromising population dynamics of these forage species, thus decreasing future secondary production (Ares, 2007; Oñatibia et al., 2015). In other words, changes in long-term grazing management, such as exclusion and intensification, first lead to negative effects on vegetation and later on domestic herbivores.

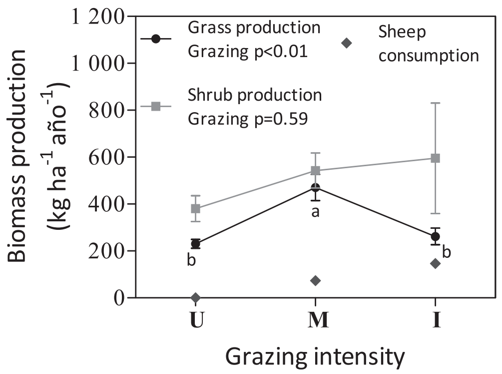

Fig. 3. Aboveground net primary productivity of grasses and shrubs under three grazing intensities (U: Ungrazed; M: Moderately grazed; I: Intensively grazed). Symbols correspond to mean values and vertical lines indicate standard errors. Different letters indicate significant differences ($P < 0.05$) among grazing intensities within each life form (Tukey test).

The vast knowledge on the natural history of this steppe system, which has been generated by over 50 years of research, allows us to discuss in depth the dominant species patterns. Among grass species we measured a sharp decrease, principally under intensive grazing in the total aboveground biomass of *P. ligularis* and *B. pictus*, which are the two most preferred species in this community (Bonvissuto et al., 1983; Adler et al., 2004). Their forage value (Easdale and Aguiar, 2012) supports their inclusion in a list of critical species for the sustainability of livestock farms. However, live biomass of *P. ligularis* did not diminish in moderately grazed sites compared with those ungrazed, indicating that moderate grazing could be promoting green biomass production of this species, thus compensating defoliation. *P. speciosa* increased under moderately grazing conditions overcompensating more preferred species slight reduction. However, under intensively grazed conditions, this species also decreased significantly. This supports the notion that although *P. speciosa* is not a highly preferred species (Bonvissuto et al., 1983), sheep switch to consuming it given that other valuable forage species decrease or disappear. *P. humilis* was the only species that showed an increasing trend with grazing, but without compensating the reduction in forage species under intensively grazed conditions. This unpreferred species has been considered as a healing species of the most degraded sites (Soriano, 1956). Other species were present in our study systems but their frequency in our sample was less than 20% (5% modal frequency). Therefore, it was impossible to perform robust statistical analysis (cf. Jobbágy and Sala, 2000).

There has been abundant debate about woody encroachment in arid and semiarid steppes (Sankaran et al., 2005). We found that shrub biomass was less susceptible than grass biomass to domestic grazing intensification. Total shrub biomass was not affected by sheep intensity. However, as previously stated, shrub species presented different responses to grazing, and therefore, considering a single response group is an oversimplification (Cipriotti and Aguiar, 2010). We measured that *S. filaginoides* increased its biomass and density in intensively grazed areas. Contrastingly, *A. volckmannii* and *M. spinosum* exhibited no significant changes even though we expected them to be negatively affected by grazing, being usually browsed by sheep (Bonvissuto et al., 1983; Cavagnaro et al., 2003; Cipriotti and Aguiar, 2012). This response pattern may be explained by indirect positive effects of grazing (Cipriotti and Aguiar, 2012) driven by a decrease of preferred grass cover (Perelman et al., 1997) and increase of bare soil surface (Golluscio et al., 2009). This process would raise deep soil water availability (Sala et al., 1989). The greater biomass and density of *S. filaginoides* under intensive levels of grazing and the lower values under moderate levels may be due to the fact that this unpreferred species (Bonvissuto et al., 1983; Cavagnaro et al., 2003) is a shrub that would be most affected by changes in grass biomass, since it has a shallower root system than *A. volckmannii* and *M. spinosum* (Fernández and Paruelo, 1988; Golluscio et al., 2006). Therefore, resources used or released from grass into the surface layers, mainly water (Sala et al., 1989), may impact on *S. filaginoides* demography (Cipriotti and Aguiar, 2010), which responded contrastingly to grass biomass. Finally, the high variability of *M. spinosum* biomass in intensive grazing fields may be indicative that grazing intensification could trigger different and opposite responses in this dominant shrub species, from encroachment to decrease (Cipriotti and Aguiar, 2012).

Lately, the debate about domestic grazing management in rangelands has been renewed (Briske et al., 2008; Murdoch et al., 2010; Teague et al., 2013). This study shows that in this Patagonian steppe, exclusion of grazing is not the best strategy for the socio-ecosystems as was proposed by Murdoch et al. (2010). Moreover, our results support the idea that in arid communities, where plant growth is limited mainly by precipitation or water availability and not by defoliation frequency (Briske et al., 2008; Bailey and Brown, 2011), continuous moderate grazing could increase productivity without major negative changes in species composition, thus herbivores can increase their own food. However, continuous grazing in large paddocks, even under moderate stocking rates, can produce a gradual decline in rangeland condition, mainly due to an uneven grazing distribution. In this sense the regulation of stocking rate should be performed along with practices that improve grazing distribution (Bailey and Brown, 2011). In addition, the results here also indicate a potential risk of management of natural vegetation through grazing, because inadequate regulation of the stocking rate could shift composition of biomass towards a dominance of species avoided by sheep (Cingolani et al., 2005) and it could reduce productivity.

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